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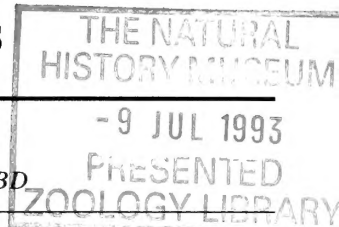
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A new snake from St Lucia, West Indies

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SYNOPSIS. The *Clelia clelia* reported from Dominica and St Lucia are reinvestigated. The specimens concerned are recognised as a new species, *Clelia errabunda*. It is derived in relation to the mainland species *C. bicolor* and *C. rustica* and is the primitive sister species of the mainland *C. clelia*, *C. equatoriana* and *C. scytalina*. As such it is interpreted as an island relict. Records from Dominica and Guyana are rejected, the St Lucia records are confirmed.

INTRODUCTION

Nearly a hundred years ago Boulenger (1896) reported the South American snake *Oxyrhopus clelia*, now known as *Clelia clelia*, from the Windward Islands of Dominica and St Lucia, as well as from mainland localities. Ever since then this species has been listed for these two islands, either in the genus *Clelia* (Barbour, 1930; Schwartz & Henderson, 1988) or *Pseudoboa* (Barbour, 1935, 1937). There are other records of this snake for St Lucia but this remains the only record for Dominica.

Boulenger (1896) distinguished two varieties of '*Oxyrhopus clelia*': A, with 19 scale-rows at mid-body, and B, with 17 scale-rows. Under variety 'B' Boulenger lists: two specimens from 'The city of Mexico', three specimens from 'W. Ecuador' and one specimen each from 'Demerara', 'Dominica' and 'St Lucia'.

Bailey (1970, in Peters & Orejas-Miranda) gives a key to the mainland species of *Clelia*. The city of Mexico specimens key out as *Clelia scytalina*, the Ecuador specimens as *C. equatoriana*. The remaining three specimens reach the *scytalina-equatoriana* couplet of the key but are not clearly assignable to either mainland species. Boulenger's variety 'A' specimens key out as *C.c.clelia* and *C.c.plumbea*, the two subspecies recognised by Bailey. *Clelia* was later reported from the island of Grenada. It was described by Greer (1965) as *Clelia clelia groomei*; Bailey places this in the synonymy of *C.c.clelia*.

Further examination of these remaining three specimens shows that they represent an unrecognised species. In the hope of determining the affinities of the new form the specimens of *Clelia* in the collection of The Natural History Museum, London were examined. A Paris Museum specimen from St Lucia was also examined. The seven species recognised by Bailey are represented. It should be noted that Scrocchi and Viñas (1990) have now sunk *occipitolutea* in the synonymy of *clelia*.

MATERIALS AND METHODS

Each specimen was examined in respect of external features, anterior viscera, maxillary teeth and, in the case of males, hemipenis. For a representative of each species dissections were made to show the superficial jaw muscles, ligaments and

labial glands and the upper and lower jaws.

The ventral scale count is according to Dowling (1951). The notation for the scale-rows on the trunk allows a detailed record in a single line of type using characters on a word processor keyboard. An oblique transverse scale-row is identified by the ventral scale from which it passes backwards, as shown by M.A. Smith (1943, fig. 10). Where there is a scale-row fusion the upper of the two merged rows is indicated. For example male specimen BMNH 89.4.8.2 is recorded as:

V 210 >>5> 17 (36;5</33;5<) 19 (145;4>/142;4>) 17

Ventral scale count 210. Three scale-row fusions from the back of the head onto the neck, the third recognisable as due to the fusion of row 5 with the row below. Seventeen rows on the neck through oblique row 36 left/33 right; row 5 splits giving rise to 19 rows through oblique row 145 left/142 right; row 4 merges with row below giving 17 rows. Most specimens were recorded down the left-hand side only (Table 1, see Appendix).

The subcaudal count starts with the first scale on the left side which makes full contact with a scale obliquely forward and opposite. The dorsal scale-rows on the tail are somewhat irregular around the base but settle down to even row stretches: 8, 6, 4, 2. The fusions are rarely symmetrical so that there are short odd number transitions between the even stretches. Each transition is included in the preceding, higher, even row stretch. The transverse rows are identified by the subcaudal scale-row pairs from which they arise obliquely. The tail of the above specimen was recorded as:

79 prs, >8 (10) 8 (25) 6 (45) 4 (73) 2

More than eight longitudinal rows through oblique row ten, eight (and seven) through row 25, six (and five) through row 45, four (and three) through 73 and two rows to the terminal scute. From this record the lengths of the five stretches are calculated as the basis of comparison of the individual specimens. The above becomes:

C 79 >8:10 8:15 6:20 4:28 2:6

This feature shows marked sexual dimorphism.

For selected specimens scales were mounted on slides to be examined for the presence of pits and tubercles (Underwood, 1963). The wet scales are laid on a dried film of polyvinyl alcohol lactophenol mounting medium. When dry the slide is then covered using Canada balsam. For each specimen the

scales mounted are the frontal, a parietal and a vertical series of scales at about mid-trunk from row one to the vertebral.

The immunological studies of Cadle (1984) suggest that species of *Pseudoboa* are sister to *Clelia*; his sample included the type species of each genus. He also found that *Oxyrhopus fitzingeri* is closer to *Clelia* plus *Pseudoboa* than it is to other species of *Oxyrhopus*. '*Oxyrhopus*' *fitzingeri* is therefore included as part of the outgroup. In the absence of an analysis, the majority outgroup condition is taken to be primitive for the ingroup.

The four species of *Pseudoboa* recognised by Bailey share the special feature of single subcaudals. No evident special feature unites the species of *Clelia*. On further study the boundary between the two genera may be redrawn, or abolished so that the assignment of the species discussed here may be changed.

The loreal is rather variable. It may be about as large as the preocular, in which case it meets supralabials two and three. It may be smaller and may meet only supralabial two. It may be absent allowing the prefrontals to meet the supralabials, or the nasal to meet the preocular (as a unilateral variant, *C. clelia* BMNH 89.4.8.2). A large loreal is assumed to be primitive.

Boulenger (1896) distinguishes between those *Oxyrhopus* (s.l.) in which the preocular reaches the upper surface of the head and those in which it does not. The distinction appears to be real but it can be influenced by the condition of the specimen and by the angle of view. The supraocular scale meets the preocular and often, also, the prefrontal scale. The lengths of the supraocular-preocular and the supraocular-prefrontal sutures are compared. The prefrontal suture may range from two or three times the length of the preocular suture, as in *Clelia rustica*, to absent, as in *Oxyrhopus petola* in which the preocular meets the frontal.

There are one preocular and two postoculars. The temporals are 2:3. The upper anterior temporal always meets postoculars; the lower may meet them (represented by $+/-2:3$) or may not meet them ($+/-2:3$). In every species represented by more than two specimens this contact is variable. Where the temporal does not make contact the labial scale is higher than its neighbours. However, *rustica* is nearly constant, on only one side of one of nine specimens does the lower temporal make contact (BMNH 95.9.17.21). The outgroup is also variable so polarity is uncertain. In one *rustica* there is no suture between prefrontal and preocular (BMNH 86.1.19.21).

There may be three or two anterior supralabials. As three is the commonest number in the outgroup it is assumed to be primitive. There are two supralabials meeting the eye and three postocular supralabials. Anterior and posterior infralabials are distinguished. The last anterior infralabial is pentagonal; from it starts the posterior row and a mesial row. The anterior infralabials are usually five. Four and six occur as unilateral variants; one *rustica* (BMNH 1909.11.2.16) has four symmetrically. The posterior infralabials range from four to two. As four is the commonest number in the outgroup this is assumed to be primitive.

The genials range from posterior about as large as the anterior to somewhat smaller. This does not appear to be a taxonomically useful feature.

There are always two, sometimes three, scale row fusions from the back of the head onto the neck. The rows on the neck may be 19 or 17. As a majority of the outgroup have 19 this is inferred primitive. In those with 19 rows this number

continues through mid-body and then reduces by fusion of row four or five with the row below to 17 rows. The vertebral or paravertebral rows were not seen to be involved in scale-row changes. Those with 17 neck rows may continue without change to the end of the trunk. In some specimens, however, a lateral row splits on the posterior neck to give rise to 19 rows through mid-body, then reducing to 17 rows. Such a minimum on the neck rising to a maximum around mid-body and falling towards the vent is widespread in henophidian grade snakes (Underwood and Stimson, 1990). However, this condition is found in none of the outgroup so it is here assumed to be a derived, pseudoprimitive feature. The scale-row pattern is scored as 19:19:17 (inferred primitive), 17:19:17 or 17:17:17.

In some specimens the vertebral scale-row is undifferentiated, but in many it is wider than the paravertebral rows. This modification is a little more pronounced towards the posterior trunk. As most of the outgroup have undifferentiated vertebral scales this is assumed to be primitive.

These snakes usually have both scale pits and tubercles (Underwood, 1963). The pits are confined to the apices of the scales of the trunk and tail, where they usually occur in pairs. Tubercles may be numerous on the head scales. On the trunk they are rather irregularly distributed around the centre of each scale; numbers range from five to zero (Fig. 2). Both pits and tubercles tend to be better developed on the upper scale-rows. Where the vertebral scale-row is enlarged they may be reduced or missing. Pits and tubercles are found in the outgroup and their presence is inferred primitive.

The anterior viscera were examined and their positions recorded in ventral scale units. This has the advantage that juveniles and adults can be compared. Organ positions determined by measurement are subject to allometric change (Thorpe, 1975). The features recorded are: tip of the hyoid, tip of the ventricle, anterior end of the liver and the end of the tracheal cartilages. In all the entry of the trachea into the right lung is terminal. This is a derived condition which Wallach (personal communication) reports to be general in Xenodontine snakes. In all there is some extension of the vascularisation of the lung into the roof of the trachea, but it does not extend far forwards of the heart. The left lung may be present but small, up to about one or two scale-units long and vascular; it may be a non-vascular vestige or it may be absent. Presence is inferred primitive.

The trachea may terminate no more than three or four scale-units beyond the tip of the heart. It may extend to overlap the liver, in some cases extending the full length of the vascular portion of the lung to reach the terminal air-sac. A short trachea is inferred primitive.

Counts are made of the teeth, and empty tooth places, of the left maxilla. The solid teeth show a moderate increase in size from front to rear. They are followed by an interval and two obliquely placed teeth with anterior grooves (Fig. 3). Polarity is not inferred. In one juvenile specimen (*clelia*, BMNH 1933.6.24.102) no grooves could be seen, even when the maxilla was removed and dried. The anterior tooth count is recorded. For sample specimens counts were made of the teeth on the dentary, palatine and pterygoid bones. They all have a full length choanal process of the palatine bone with a broad base, about half the length of the palatine, which sweeps backwards into a process which overlaps the pterygoid bone by two to three teeth (Fig. 3). The maxillary process of the palatine is turned backwards; it bears a

foramen for the maxillary nerve which emerges on the underside anteriorly.

For sample specimens the skin on the side of the neck was turned forwards to expose the superficial jaw muscles and ligaments and the labial glands. The most superficial muscle, which is easily damaged, is the constrictor colli (Haas, 1973). In the outgroup this is a thin sheet of muscle which passes from about the level of the head of the quadrate backwards and downwards over the jaw articulation to insert on the skin of the throat. In the species of *Clelia* examined the muscle follows a similar course, the anterior portion has a diffuse origin on the surface of the adductor externus profundus muscle. The posterior portion arises on the head of the quadrate; this is inferred derived (Fig. 4).

The cervico-mandibularis muscle arises from the back of the neck and passes downwards and forwards to insert on the articular head of the quadrate (Fig. 4). This appears to be a primitive condition. From the articular head of the quadrate arises a ligament which passes forwards and divides. The lateral, labial portion inserts on the posterior supralabial scales and onto the capsule of Duvernoy's gland. It peels off the supralabial scales rather more easily than is usual in snakes; this is thought to be derived. The mesial, maxillary ligament passes forwards to insert on the posterior lateral corner of the maxilla.

undifferentiated vertebral scale row, no left lung and a short trachea extending no more than five ventral scale units beyond the tip of the ventricle. Distinguished from *rustica* and *bicolor* by absence of a left lung. Distinguished from *clelia*, *equatoriana* and *scytalina* by the undifferentiated vertebral scale-row and short trachea. Further distinguished from *clelia* by 17 scale-rows from neck to vent.

Holotype: BMNH 89.8.14.25, male, St Lucia, West Indies, collected by G.A. Ramage, presented by West Indies Exploration Committee; snout-vent c.112 cms, tail 32 cms with extreme tip missing.

Paratype: MNHP 7598, male, St Lucia; snout-vent c.116 cms, tail 29+ cms with tip missing.

Referred specimens: BMNH 89.8.14.12, female, 'Dominica', West Indies, collected by G.A. Ramage, presented by West Indies Exploration Committee, snout-vent 138 cms, tail 27.6 cms.

BMNH 1988.717, female, 'Demerara', presented by Capt E. Sabine, R.E., snout-vent 117 cms, much of the tail is missing.

The other species of *Clelia* are widely distributed on the South and Central American mainland and a few offshore islands (Bailey, 1970). The name is taken from the Latin *errabundus* = wandering, in reference to the occurrence of the new form well outside the range of its mainland relatives.

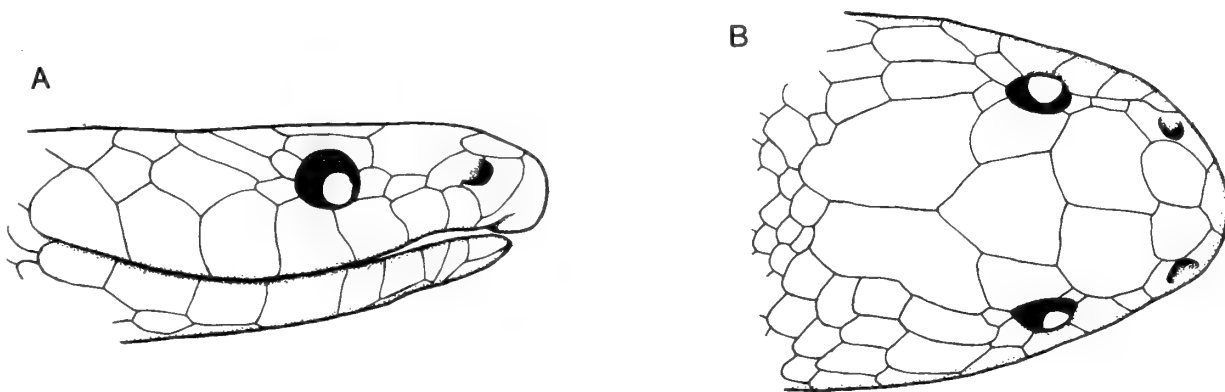


Fig. 1. *Clelia errabunda* sp. nov., type BMNH 89.8.14.25. A, lateral view of head (reversed on account of distortion of right side of head); B, dorsal view of head.

Mucous supralabial glands extend along the margin of the upper lip from the corner of the mouth to the snout. There are similar glands along the margin of the lower jaw. Mesial to the three posterior supralabial scales lies the Duvernoy's (venom) gland (Fig. 4).

At the level of the corner of the mouth, mesial to the maxillary ligament, is the organ termed anterior temporal gland by Smith & Bellairs (1947) and rictal gland by McDowell (1986). It is found in all of the species examined; it is usually visible mesial to the posterior end of the Duvernoy's gland (Fig. 4).

RESULTS

Clelia errabunda sp. nov.

DIAGNOSIS. A species of *Clelia* with uniform dark grey adult colouration of the upperside of the head, trunk and tail, extending to the lateral margins of the ventral scales, an

The type has two preocular scales on one side, seen in no other specimen of *Clelia*. All have two anterior and three posterior temporals. The lower anterior temporal scale meets a postocular in the type only. The 'Demerara' specimen has three anterior supralabial scales on the left-hand side, seen elsewhere only in *C. bicolor*. All have five anterior infralabial scales and three posterior. The anterior genials are little, if at all, larger than the posterior. The four specimens have tubercles but no pits on the head, as in other *Clelia* and *Pseudoboa*. The number of frontal and parietal tubercles is high. Most of the trunk scales bear paired apical pits, as is usual in *Clelia*, and a moderate number of tubercles (Table 2, see Appendix).

The island specimens have 14 anterior maxillary teeth (on the left), which is higher than for *clelia* and *equatoriana* (Table 3, see Appendix); the 'Demerara' specimen has 13/12. The ventral scale counts are high for *Clelia*, but not extreme. The subcaudal scales are entirely paired, save that the last one is single in the 'Dominica' specimen. Apart from the difference of sex the three island specimens are very similar.

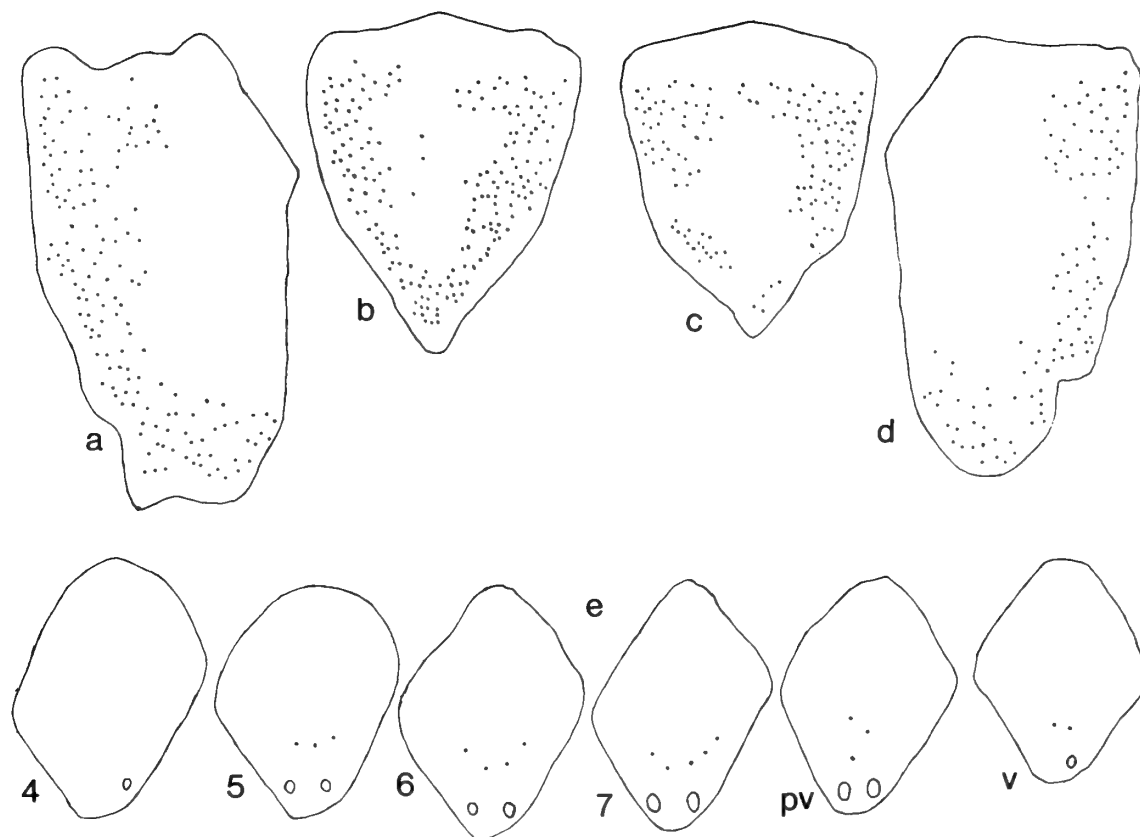


Fig. 2. *Clelia errabunda* sp. nov., mounted scales to show distribution of tubercles and pits. a,b, parietal and frontal of BMNH 89.8.14.12; c,d, frontal and parietal of BMNH 89.8.14.25 (type); e, mid-trunk scales of BMNH 89.8.14.12, from rows: 4, 5, 6, 7, paravertebral and vertebral. The lower rows lack scale-organs.

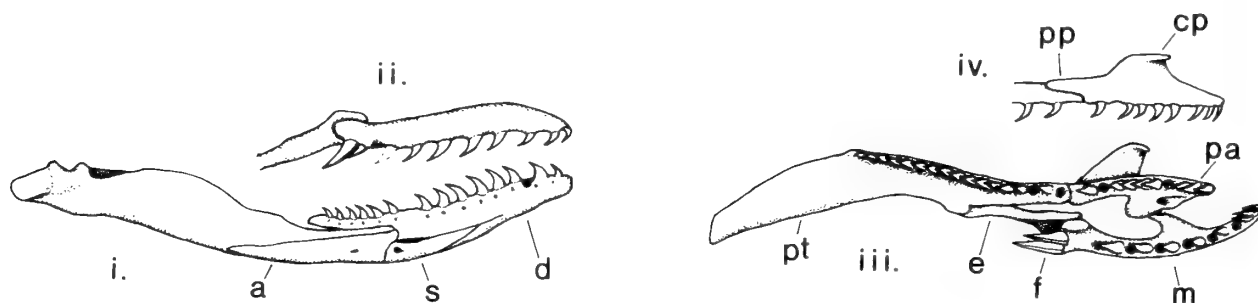


Fig. 3. *Clelia errabunda*, BMNH 85.8.14.12. i, mesial view of lower jaw: a = angular, d = dentary, s = splenial; ii, lateral view of left maxilla (reversed); iii, ventral view of left upper jawbones: e = ectopterygoid, f = fangs with grooves, m = maxilla, pa = palatine, pt = pterygoid; iv, mesial view of left palatine-ptyergoid articulation: cp = choanal process, pp = posterior process of palatine.

The 'Dominica' female has 234 ventrals and 71 subcaudals: total 305. The type male has the extreme tip of the tail missing, judged to be not more than two pairs of subcaudals. It has 221 ventrals and 82 + (?)2 subcaudals: total 303 + (?)2. The paratype male has 224 ventrals and 75+ subcaudals. The 'Demerara' female has 230.5 ventrals and only 36 remaining pairs of subcaudals.

The 'Dominica' specimen has a Duvernoy's (venom) gland from behind the eye to the corner of the mouth; it is as high as the supralabial scales plus the lower temporal scales. The hemipenes of the two males are 18 subcaudal scale units long, there are prominent lobes on a shaft 13 units long. The sulcus spermaticus forks on the shaft at scale six (type) or seven (paratype). Proximally on the shaft there are very fine spines

and, in the retracted organ, longitudinal folds. From scale nine to the cleft there are large spines, about 26 in the type and 38 in the paratype; these are high counts for *Clelia*. At the base of each lobe there is a large spine, as is usual in *Clelia*. the branch sulcus passes down the middle of an area of large calyces with a clear margin (a capitulum).

Inspection of The Natural History Museum register raises a doubt about the provenance of the Dominica specimen. G.A. Ramage brought back a collection of herpetological specimens from Dominica and St Lucia. These were registered in 1889. They are entered in Boulenger's hand. The register starts (with present identifications substituted):

89.8.14. 1-8 *Typhlops dominicana* Dominica, June '89

9–11	<i>Alsophis antillensis sibonius</i>	Dominica, June '89
12	<i>Clelia errabunda</i>	Dominica, June '89
13	<i>Bothrops caribbaeus</i>	Dominica, June '89
14	<i>Thecadactylus rapicauda</i>	St Lucia, April '89

There follow another eight species attributed to St Lucia, including the St Lucia endemics *Hyla rubra*, *Sphaerodactylus microlepis*, *Anolis luciae* and *Liophis ornatus*. these St Lucia attributions are not therefore in question. Boulenger's St Lucia entries are interrupted by four fish entries in a different hand.

The *Typhlops* and *Alsophis* are forms endemic to Dominica. What, however, attracts attention is the record of *Bothrops* from Dominica. We may be sure that if a pit-viper were living on this island there would have been further reports since 1889. It is clear that the *Bothrops* was mistakenly attributed to Dominica. The specimen of *Clelia* appears to be the only documented record of the genus from Dominica. Is this attribution to Dominica also a mistake? On the other hand there are several further specimens of *Clelia* from St Lucia in the Museum of Comparative Zoology.

In addition to *Alsophis antillensis*, there is no more than hearsay evidence of a second species of black snake on Dominica. Bullock & Evans (1988) list *Clelia clelia* on Dominica as 'Tete-chyen nwe'. Dr Bullock writes that he has not seen *Clelia* but he has reports from informants whom he regards as reliable. Dr R. Thorpe, Miss A. Malhotra and Mr M. Day have come across no evidence of *Clelia* on the island. On Dominica it would be distinguished from *Alsophis* by the uniform black dorsal colouration and by 17 dorsal scale rows on the anterior trunk. The *Alsophis* has some irregular yellow markings and 19 scale rows anteriorly. Unless and until there is clear evidence of the occurrence of *Clelia* on Dominica it should be dropped from the island list. Barbour (1930) says of '*Clelia clelia*' that "This species is surely extinct on St Lucia. . .". Long (1974) writes that "the cribo no longer exists in St Lucia. . .". Dr D. Corke also reports that he has found no trace of the survival of *Clelia* on St Lucia.

Even greater doubts arise about the provenance of the 'Demerara' specimen of *errabunda*. The specimen had no original registration number; the Museum register starts in 1837. A search of the early entries shows no record of specimens from E. Sabine. The Museum archivist reports that the trustees' minutes record donations from Capt Sabine between 1818 and 1824 with, however, no indication of any from the Caribbean.

The collection has other snakes from 'Edw. Sabine'. There is a male *Xenodon merremi*, a species widely distributed in South America and known from Guyana on the basis of other specimens. There are a male and a female of *Oxyrhopus trigeminus*, not otherwise known from this part of South America.

There are also two lots of *Bothrops*. A female from 'Capt Sabine, Berbice' and two females and a male from 'Col Sabine, Demerara'. These were compared with specimens of *B. atrox* and *B. brazili* from Guyana and with *B. caribbaeus* from St Lucia. With ventral and mid-body counts of: M 201:26, F 205:27, F 206:29 and F 210:29 they fall within the range of counts reported by Lazell (1964) for *caribbaeus*. The postocular stripe passes across the last supralabial scale dorsal to the corner of the mouth as in *caribbaeus*. The ventral scales are laterally peppered with dark spots, as in *caribbaeus* and

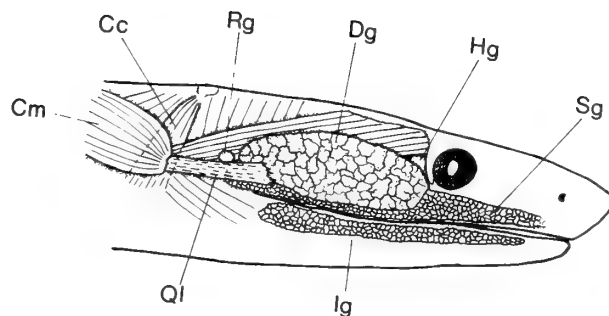


Fig. 4. *Clelia errabunda* sp. nov., BMNH 89.8.14.12. Dissection to show superficial head muscles and glands (reversed).

Cc = constrictor colli muscle, overlaying other structures;
Cm = cervico-mandibular muscle; Dg = Duvernoy's gland;
Hg = Harder's gland; Ig = infralabial gland;
Ql = quadrato-labial ligament; Sg = supralabial gland;
Rg = rectal gland.

brazili and unlike *atrox*. In all, the dorsal bands are indistinct. In two of the Demerara specimens the bands can be seen to have parallel sides or to converge towards the dorsal midline as described by Lazell for *caribbaeus*. The third shows some diverging bands. The Guyana *atrox* have dark patches on the lower flanks which extend onto the ventrals unlike these Sabine specimens. The *brazili* have dark bordered bands which converge towards the midline. These observations suggest that the 'Berbice' and 'Demerara' specimens are most probably *caribbaeus*, a species known only from St Lucia. The above considerations raise a doubt that Sabine collected any specimens in Guyana.

It is evident that Sabine was long enough, supposedly in Guyana, to achieve promotion from captain to colonel; in that time he may well have visited St Lucia. The locality of the 'Demerara' *Clelia errabunda* is therefore discounted. The uniform 17 scale-rows and undifferentiated vertebrae would distinguish it from local *Clelia clelia*.

Dumeril, Bibron & Dumeril (1854) report that the Paris museum has specimens of '*Brachyruton cloelia*' from Guyana, Brazil, Mexico and Guadeloupe. The 'Guadeloupe' specimen (MNHP 169) is a hatchling with counts V200, C83 and 19:19:19 scale rows. The tip of the heart is at V46, the trachea extends beyond V90. This is clearly a specimen of *Clelia clelia*, with an unusually low ventral count. The locality is undoubtedly erroneous.

In the Proceedings of the Philadelphia Academy for 1870 it is reported that Cope "called attention to a large specimen of *Trigonocephalus* (= *Bothrops*) from St Lucia, of which some fourteen inches was enclosed in the oesophagus and stomach of a larger *Oxyrhopus plumbeus* (= *Clelia clelia*).". Later Cope (1876) wrote that, as he had previously observed, he had received a specimen of *Clelia clelia* from Martinique(!) which had swallowed a large *Bothrops*. Malnate (personal communication) examined the specimen(s). It is ANSP 10220 from 'Santa Cruz', received from Mrs J.L. Endicott. 'Santa Cruz' presumably means St Croix in the Virgin Islands! It is unlikely to be a St Lucia locality; most of the place names are French. This one specimen thus has three different geographical attributions!

Malnate reports that the *Clelia* has 17 scale-rows throughout and an undifferentiated vertebral scale row; it therefore fits *C. errabunda*. The half-swallowed *Bothrops* has 25 scale rows about midbody, falling to 19 rows. Lazell (1964) gives

mid-body scale-row counts for *Bothrops caribbaeus* from St Lucia as 25–29 (mode 27) and for *Bothrops lanceolatus* from Martinique counts from 29–33 (mode 31). The Philadelphia Academy specimen, with 25 rows, is at the lower end of the range for St Lucia specimens. Beyond reasonable doubt therefore Cope had a specimen of *C. errabunda* which had half swallowed a St Lucia *Bothrops caribbaeus*.

Relationships of *Clelia errabunda*

The species currently assigned to *Clelia* can be arranged at several levels on the basis of the derived states of the respiratory system, the vertebral scale row and the ventral scale counts. This is set out in Table 3.

C. bicolor. The three anterior supralabials, the low ventral scale counts, the undifferentiated vertebral scales, the presence of a left lung and a short trachea are primitive features. The high maxillary tooth count appears to be a derived feature.

C. rustica. This species also has undifferentiated vertebral scales, a left lung (a mere vestige in BMNH 81.7.2.9) and a short trachea. *C. rustica* and the following species are derived in relation to *bicolor* in respect of two anterior supralabials and higher ventral counts.

C. errabunda, *clelia*, *equatoriana* and *scytalina* share the derived feature of absent left lung. The latter three species are further derived than *errabunda* in respect of the enlarged vertebral scales and extended trachea.

The type specimen of *Clelia clelia* Daudin (1803) is not known to survive; however, the type locality is given as 'Suriname'. It is therefore assumed that specimens from the northern coast of South America are typical *clelia*. Specimens in The Natural History Museum from this area, from Central America, from Rio Condoto on the Pacific slope of Colombia

(1), from La Paloma nr Santiago R., Ecuador (1) and from most of the rest of South America show the 19:19:17 scale row pattern. However, a second specimen from Rio Condoto and specimens from Ecuador (Guayaquil and east of Loja, 2), Peru (3) and Manacapuro on the Amazon (1) show the 17:19:17 scale-row pattern. These are indistinguishable from typical *clelia* in respect of the other characters considered here. Their occurrence in a north-western area of South America with near overlap with the 19:19:17 (Rio Condoto) form on the Pacific slope of Colombia does not look like an accident of sampling (Fig. 5). The form in eastern Brazil (*plumbea*) lacks spines on the hemipenis, some specimens from the southern part of the range (*occipitolutea*) are pale in colour, so *clelia* is evidently a variable species. Roze (1959) reports a specimen from Venezuela with counts of: 21:22:19:17 and Chippaux (1986) reports a specimen with 21:19:17 rows from French Guyana.

After the above account was prepared I received from Zaher (personal communication) a photocopy of a portion of Bailey's unpublished PhD thesis. It is evident that at that time he regarded the island *Clelia* as sufficiently distinct to merit subspecific status. He too did not believe the Guyana localities of the Sabine specimens.

DISCUSSION

The species *clelia*, *equatoriana*, *scytalina* and *errabunda* share uniform dark adult colouration and absence of a small left lung. Most other pseudoboine snakes have a small left lung and a more varied colour pattern. Within this group of four species *errabunda* is primitive to the others in that the vertebral scale row is not enlarged and the trachea is short.

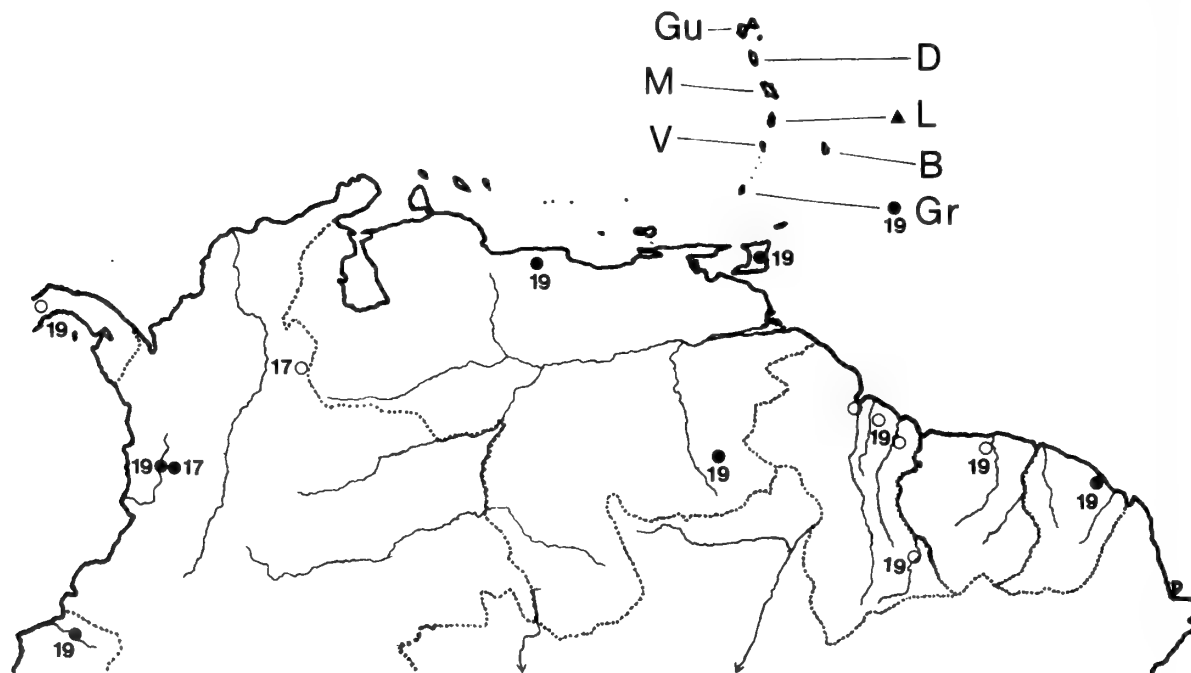


Fig. 5. Localities of specimens from northern South America and the Lesser Antilles. Solid symbols = precise localities; hollow symbols = approximate localities; circles = *Clelia clelia*; triangle = *Clelia errabunda*; 17, 19 = no of scale rows on neck of *C. clelia*. B = Barbados, D = Dominica, Gr = Grenada, Gu = Guadeloupe, L = St. Lucia, M = Martinique, V = St. Vincent.

Because the 19:19:17 scale row pattern is widespread in pseudoboinae snakes and is also found in most *Clelia* we may infer that it was the condition of the ancestor of this species group. The 17:17:17 pattern shown by *errabunda* would thus be interpreted as a derived feature setting it apart. However, the occurrence of the 17:17:17 pattern in *equatoriana* and *scytalina* and the 17:19:17 and 21:19:17 patterns within *Clelia* suggests that little significance can be attached to the scale-row pattern. The most nearly special feature of the new species is the high number of large spines on the hemipenis. Otherwise it is close to the status of what Ackery and Vane-Wright (1984) call a 'paraspecies', without any special feature setting it apart. The short trachea and unmodified vertebral scales by which it is distinguished are primitive features found in hundreds of other species of snakes.

Greer (1965) reports that the Grenada *Clelia* is diurnal, unlike its mainland relatives. *Clelia clelia* from Grenada is otherwise little different from mainland *Clelia*; this is confirmed by Wallach's report (personal communication) that it has an extended trachea. It is presumably a relatively recent immigrant from South America. On the other hand *errabunda*, on St Lucia, is primitive to the mainland members of the *Clelia* group. This suggests that it colonised St Lucia at an early date and that its ancestral stock was later replaced on the mainland by the more derived *Clelia*. It is an example of a primitive form surviving as an island relict.

Boa constrictor occurs on St Lucia and Dominica. The two island populations and the mainland form are well differentiated from one another and are recognised as separate subspecies (Lazell, 1964). The pit-vipers, *Bothrops*, on the adjacent islands of St Lucia and Martinique are sufficiently differentiated that they are recognised as full species by Lazell (1964). For both *Boa* and *Bothrops* this suggests either separate colonisation of the islands from the mainland or colonisation of one island and passage to the other long ago. There is at present no evidence that these are primitive island relicts.

Cope (1870) is reported as saying that the "islands of Martinique and Guadeloupe had become so infested with the fer-de-lance" (*Bothrops lanceolatus*) "as to be in parts almost uninhabitable, and it was chiefly on account of the danger from this venomous reptile that collecting naturalists of late years had so seldom visited them"! "Some means had been adopted to check the increase of this pest, but with small results". "Prof Cope thought that as the *Oxyrhopus plumbeus* (= *Clelia clelia*) was very numerous in Venezuela and Brazil, and since it was very harmless and easily procured, that its introduction in large numbers into Martinique, etc, would be a simple matter, and one probably to be attended with good results in the diminution, at least, of this enemy of agriculture".

Lazell (1964) tells us that on both Martinique and St Lucia the local *Bothrops* is known as 'serpent'. We may speculate that prior to human arrival 'serpents' were already established on St Lucia before the 'cribo' (*Clelia*) arrived to prey upon them.

It is said that the mongoose was introduced into St Lucia in the hope that it would reduce the *Bothrops*. Today, although the mongoose may eat *Bothrops*, it also eats domestic poultry. Following human disturbance, it is ironic that the indigenous 'pest', the 'serpent', is supplemented by an introduced pest, the mongoose, and the indigenous biological control, the 'cribo', is extinct! In the absence of this 'control' Lazell (1964) reports that in some areas of St Lucia the serpent is 'abundant beyond belief'.

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APPENDIX

Table 1 Some representative specimens of *Clelia*, showing: sex, ventrals, scale row reduction pattern, scale row stretches on tail. * = type specimen of *Oxyrhopus maculatus* Boulenger.

				Tail row stretches					
	V	Row reductions	C	>8	8	6	4	2	
<i>scytalina</i>									
	68.4.7.7	M 212	>>19(12;5>)17	75	15	11	20	25	4
	68.4.7.8	F 209	>>>19(7;5>)17	83	11	14	22	30	6
<i>equatoriana</i>									
	60.6.16.47	M 201	>>17	75	5	17	23	30	0
Geneva	2410.9	M 201	>>17	69	4	14	18	28	5
	60.6.16.48	F 217	>>17	–	3	12	20	–	–
	60.6016.49	F 219	>>17	–	5	12	21	–	–
<i>clelia</i>									
	74.8.4.56	M 216	>>17(44;5<)19(149;5>)17	91	10	19	26	26	10
	90.10.6.29	M 214	>>>17(41;4<)19(146;5>)17	71	6	20	27	18	0
	1926.4.30.14	F 238	>>17(43;4<)19(159;4>)17	82	2	8	24	26	12
	51.7.17.136	M 219	>19(165;4>)17	91	6	20	24	33	8
	86.10.4.12	M 213	>>19(165;4>)17	64	12	13	19	17	3
	1929.10.19.2	F 237	>19(209;5>)17	84	3	14	32	30	5
	1902.7.29.68	F 231	>>19(142;6>)17	55	3	7	25	20	0
	* 84.2.23.40	F 213	>>19(179;5>)17	50	3	11	20	19	0
<i>errabunda</i>									
	89.8.14.25	M 221	>>17	84	11	15	22	34	0
	MHNP 7598	M 224	>>17	75+	15	14	21	25+	–
	89.8.14.12	F 234	>>17	71	5	8	27	31	0
	1988.717	F 230.5	>>(7;4>)17	–	4	11	–	–	–
<i>rustica</i>									
	86.1.19.21	M 206	>>19(176;5>)17	61	14	22	16	9	0
	81.7.2.9	M 196	>>>19(129;4>)17	60	6	23	17	16	0
	95.9.17.21	F 212	>>19(177;4>)17	55	7	17	19	12	0
	1933.9.5.7	F 195	>>19(128;4>)17	39	3	9	21	6	0
<i>bicolor</i>									
	1927.8.1.234	F 178	19(96;5>)17	59	3	15	15	21	5
	1980.1651	F 177	19(108;4>)17	58	3	12	16	23	4

Table 2 Distribution of tubercles on the dorsal, frontal and parietal scales of some selected specimens of *Clelia*.

		Dorsal scale-row nos.										fr	par
		1	2	3	4	5	6	7	8	9	10		
<i>scytalina</i>	68.4.7.7	M	–	–	4	1	4	2	1	5	4	117	98
<i>equatoriana</i>	60.6.16.47	M	–	1	–	–	1	1	1	1	2	129	98
<i>clelia</i> 19:19:17	1930.10.10.188	M	–	–	–	–	–	–	2	3	2	151	104+
<i>clelia</i> 19:19:17	94.3.14.60	F	1	3	1	1	4	2	4	4	3	96	87
<i>clelia</i> 17:19:17	89.4.8.2	M	2	3	–	2	3	3	3	4	6	150	112
<i>errabunda</i> St L.	89.8.14.25	M	–	–	–	–	–	1	2	–	–	138	92
<i>errabunda</i> St L.	MNHP 7598	M	–	–	–	–	–	1	2	–	–	200	104
<i>errabunda</i> ‘Dominica’	89.8.14.12	F	–	–	–	–	3	4	5	3	2	186	152
<i>errabunda</i> ‘Demerara’	1988.719	F	–	–	–	1	1	1	1	2	–	141	132
<i>rustica</i>	1909.11.2.16	M	–	–	–	–	–	–	–	–	–	72	45+
<i>bicolor</i>	1980.1651	F	–	–	–	–	–	1	1	1	1	45	34

Table 3 Comparison of *Clelia* species.

	n	suplabs	V	C	Max teeth	L.lung	Trachea	Vert. row
<i>scytalina</i>	F 1	2:2:3	209	83	13	+	+	+
	M 1		212	75	14			
<i>equatoriana</i>	F 2	2:2:3	217–219	–	11.5	+	+	+
	M 2		201	72	12			
<i>clelia</i>	F 15	2:2:3	213–228–238	50–73–84	11.5	+	+	+
	M 13		204–215–226	64–82–91	11.3			
<i>errabunda</i>	F 2	2:2:3	231–234	71	14	+	–	–
	M 2		221–224	84	13.7			
<i>rustica</i>	F 7	2:2:3	195–208–231	39–44–55	11.3	–	–	–
	M 2		195–210–223	61	13.0			
<i>bicolor</i>	F 2	3:2:3	177–178	58–59	15.5	–	–	–

V = ventrals, C = subcaudals, min-mean-max; mean no of anterior maxillary teeth; – = primitive, + = derived state of left lung, trachea and vertebral scale-row.

Anatomy of the Melanonidae (Teleostei: Gadiformes), with comments on its phylogenetic relationships

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SYNOPSIS. The osteology and part of the soft anatomy of the gadiform family Melanonidae, represented by the genus *Melanonus* Günther, 1878, is described. *Melanonus* has several derived (autapomorphic) sensory features but only three osteological ones. Although contained within the Gadiformes the family is excluded from both the Macrouroidei and Gadoidei in lacking a modified palatine and enlarged intercalar and thus represents their sister-group designated as the Melanonoidei. The Suborder Gadoidei now comprises two families of uncertain phylogenetic affinity (Bathygadidae and Steindachneriidae) and two Superfamilies, Moridoidea and Gadoidea.

INTRODUCTION

The gadoid genus *Melanonus* Günther 1878 contains two species, *M. zugmayeri* Günther, 1878 (Fig. 1), and *M. gracilis* Norman, 1930, which together give a broad latitudinal, circumglobal distribution (Cohen et al., 1990; Howes, 1991a). *Melanonus* are relatively small fishes, the largest seen being 230mm total length and, oddly for gadoids, are meso-bathypelagic (100–3000m). Outwardly, *Melanonus* resembles a stomiatoid rather than a gadoid fish with its dark coloration, large, strongly-toothed jaws and tapering body (Fig. 1).

Until Marshall (1965) recognised (without diagnosis) a separate family for the genus, *Melanonus* had been considered to belong to the Moridae. Marshall (1965) and Marshall & Cohen (1973) contended that *Melanonus* was the most primitive gadiform (anacanthine) fish, a contention based on

the posterior position (at the forebrain) of the olfactory bulbs and a relatively unmodified caudal fin skeleton. The features Marshall & Cohen (1973) used to diagnose the Melanonidae rested on soft anatomical features, viz. an elaborate system of free ending neuromasts on the head and the corpus cerebelli extending (forward) to the optic tectum.

Apart from a few observations on the caudal fin skeleton and gill-arches and a description of its cranial muscles (see below) the anatomy of *Melanonus* has never properly been described. Gosline (1971) complained that “No account of the osteology is available. By contrast the family Gadidae has received more attention from anatomists than almost any other family of fishes”. Despite these shortcomings several assertions as to the phylogenetic position of the Melanonidae have been made.

Rosen & Patterson (1969) cited Marshall (1965; 1966) to the effect that *Melanonus* represents a primitive gadoid.



Fig. 1. *Melanonus zugmayeri* specimen BMNH 1991.7.9:729–30, 200mm SL, lateral view.

Schwarzahns (1980; 1984) combined the Melanonidae and Moridae (produced as a cladogram in Patterson & Rosen, 1989) and Cohen (1984) and Fahay & Markle (1984) also suggested a relationship with the Moridae, again based on the primitive arrangement of the caudal fin skeleton. Markle (1989) revised his earlier views and placed the Melanonidae near the base of his cladogram making it (with the exception of the Ranicipitidae) the sister group of all other gadiforms. Nolf & Steurbaut (1989) placed Melanonidae as an unresolved polychotomy with the Eulichthyidae, Macrouridae, Moridae and other gadoids. Okamura (1989) omitted the family from his gadoid classification but implied (p.137) on the basis of similar anterior rib structure that *Melanonus* is closely related to *Merluccius*. Howes (1989; 1990) also placed Melanonidae in an unresolved polychotomy, with Steindachneriidae, Bathygadidae and other gadoids. According to Howes (1990, 1991a & b) the majority of gadoid families form a monophyletic assemblage termed 'supragadoids', characterized by complete fusion of the upper hypurals into a single plate. The Macruronidae represent the plesiomorphic lineage of this assemblage with the Gadidae and Merlucciidae being the most derived families. The Melanonidae was assigned with the Bathygadidae, Steindachneriidae, Moridae and Eulichthyidae to the 'infragadoids' and in one scheme (Howes, 1991b) in alternative positions, one as the sister group to all gadoids excluding the Bathygadidae and Steindachneriidae, the other as also excluding the Moridae. The characters on which these phylogenetic positions were based are, however, ambiguous (see Discussion) and like all previous studies have suffered from lack of anatomical information about *Melanonus*. The following is an account of the osteology and other soft anatomical features of *Melanonus*.

MATERIALS AND METHODS

Specimens used for anatomical descriptions (all from BMNH collections): *Melanonus zugmayeri* Ucat. 230mm, 'Discovery' Stn 11550, 10.VII.1987, 20°25.5'N, 19°39.5'W, 775–825m; 1991.7.9:729–730, 220mm, 95mm SL, 20°25.8'N–31.4'N, 19° 39.8'W–38.0'W, 800–875m; 1991.7.9:731–733, cleared & stained, 66, 100, 130mm SL, 17°1.2'N, 19°57.8'W, 400–495m; 1987.1.21:595–596, 215mm

SL, dry skull prepared from 190mm SL, 49° 21.9'N, 11°51'W, 1090–1100m; 1987.1.21:597, 168mm SL, S.W. Bantry, 960–920m; 1981.3.16:377, 173mm SL, West Great Sole Banks; 1987.1.21:598–601, 175, 187, 193mm SL, one specimen, 165mm SL (cleared and stained), 50°02'N, 11°22'W, 910–980m; 1930.1.12:943 (Holotype) 13°58'S, 11°43'E. *Melanonus gracilis* 1887.12.7:22 (Holotype) 147mm SL, Antarctic; 1930.1.12:934–936, 97, 140, 150mm SL, 46°56'S, 46°03'W; 1988.11.4:13–20, 45, 49mm SL (cleared and stained), 35°13'–34°57'S, 17°50'–17° 48'E; 1988.11.4:2, 145mm SL, 50°17.7'S, 18°40.9'E, 300–150m; *Percopsis omiscomayus* 1973.3.20:46–8, 52mm (cleared and stained), 62mm SL, Lac Henry, Quebec, Canada; *Bregmaceros* sp. 1957.12.2:5–12, 54mm SL (cleared and stained) Senegal; *Gaidropsarus mediterraneus* Ucat. 122, 145mm (cleared and stained), Seaton Point, England.

In addition, material listed in Howes (1988, 1992) and Howes & Crimmen (1990) was re-examined.

Abbreviations used in the figures

aa	anguloarticular
aap	premaxillary articular process
ac	actinost
afc	anterior frontal crest
ap	premaxillary ascending process
ar	anterior ('chopstick-like') ribs
ard	anal fin radial
asp	autosphenotic
bb	basibranchial (numbered)
bh	basihyal
bl	Baudelot's ligament
bo	basioccipital
boc	basioccipital condyle
br	branchiostegal ray
cb	ceratobranchial (numbered)
cc	cerebellar corpus
ccr	cerebellar crest
cfc	central frontal crest
cl	cleithrum
cm	coronomeckelian bone
co	coracoid
de	dentary
dex	dorsal section of <i>epaxialis</i> muscle
dhy	dorsohyal
dr	dorsal fin ray

drd	dorsal fin radial	pc	postcleithrum
eb	epibranchial (numbered)	pfc	posterior (diagonal) frontal crest
ebt	epibranchial toothplate	phy	posterohyal
ect	ectopterygoid	pmp	postmaxillary process of premaxilla
edd	<i>erector</i> and <i>depressor dorsalis</i> muscles	pop	preopercle
ent	entopterygoid	pp	parapophysis
ep	epural	prn	prootic notch
epr	epineural	ps	parasphenoid
esc	extrascapular	psl	parasphenoid ascending laminae
epo	epioccipital	pte	pterotic
exc	exoccipital condyle	pts	pterosphenoid
exca	exoccipital cartilage	ptt	posttemporal
exf	exoccipital flange	pu	preural vertebra (numbered)
exo	exoccipital	pyc	pyloric caeca
fIX	foramen for glossopharyngeal nerve	qu	quadrate
fX	foramen for vagus nerve	ra	retroarticular
fl	facial lobe	Rcl	ramus canalis lateralis nerve
fm	foramen magnum	rd	<i>retractor dorsalis</i> muscle
foc	foramen for occipital nerves	re	rostrodermosupraethmoid
fr	frontal	sb	swimbladder
fv	<i>flexor ventralis</i> muscle	sbp	swimbladder pocket
fvi	<i>flexor ventralis inferioris</i> muscle	sc	scapular
ge	granular eminence	sca	<i>supracarinalis anterior</i> muscle
gg	gas-gland	scl	supracleithrum
go	gonad	so	supraoccipital
gu	gut	sop	subopercle
ha	haemal arch	spt	intercalar socket for posttemporal limb
hb	hypobranchial (numbered)	st	stomach
hf	hyomandibular fossa	sy	symplectic
hp	hypophysis	ul	ural centrum
hy	hypural (numbered)	v	vertebra (numbered)
iac	interarcular cartilage	vex	ventral section of <i>epaxialis</i> muscle
ic	intercalar	vhy	ventrohyal
ih	interhyal	vo	vomer
io	infraorbitals (numbered)		
iop	interopercle		
ird	<i>interradialis</i> muscle		
ki	kidney		
le	lateral ethmoid		
li	liver		
llp	lateral ethmoid-palatine ligament		
lmi	mandibular-interopercular ligament		
lt	trigeminal lobe		
mc	Meckel's cartilage		
md	mesonephric duct		
mec	mesethmoid cartilage		
met	metapterygoid		
mss	myoseptal strands supporting ribs		
mo	medulla oblongata		
nI-VII	cranial nerves		
na	nasal		
nal	first neural arch		
naap	nerve branch serving <i>adductor arcus palatini</i> muscle		
nau	acoustic nerve		
nbuc	buccalis branch of trigeminal trunk		
nio	infraorbital branch of trigeminal trunk		
nll	lateral line nerve		
nm1,2	neuromasts types 1 and 2		
nnm	nerve of supraorbital branch innervating posterior canal enclosed neuromast		
nr	nasal rosette		
nsab	supraorbital branch of trigeminal		
ob	olfactory bulb		
op	opercle		
ot	olfactory tract		
pa	parietal		
pah	parhypural		
pal	palatine		
pb	pelvic bone		
pbb	pharyngobranchial (numbered)		

ANATOMY

Neuromast pattern (Fig. 2).

Melanonus has a unique pattern of free-ending neuromasts covering the head in addition to those more usual neuromasts contained in the sensory canals. There are two morphotypes of the former: 1) the most numerous, are long, flange-like structures which occur on the skin covering the upper rim of the infraorbitals, the snout, cheek muscles, preoperculum and top of the head; 2) button-like structures confined to specific areas on the lower cheek, snout and frontal.

The flange-like neuromasts are usually arranged longitudinally and more or less in rows. In the snout region, individual neuromasts may be slightly curved or angled to the general direction of the others (Fig. 2B). On top of the head, rows are more definite and those on the snout tend to converge anteriorly where the organs close to the midline are larger than the others (exceptional is the star-shaped arrangement posterior to the medial extrascapular sensory pore in *M. zugmayeri*); the neuromasts close to the midline on the central part of the frontal are also nearly twice the length of the others (Fig. 2A). In *M. zugmayeri* the neuromasts along the anterior part of the supraoccipital have a regular arrangement (Fig. 2A) but in *M. gracilis* they form a pocket or enclosed area. Distribution on the preoperculum is irregular and sometimes sparse (the skin is often missing from this region and it is not possible to make precise counts).

The pitlines of button-like organs are in a double row near the border of the snout, in a patch above the nares, as an

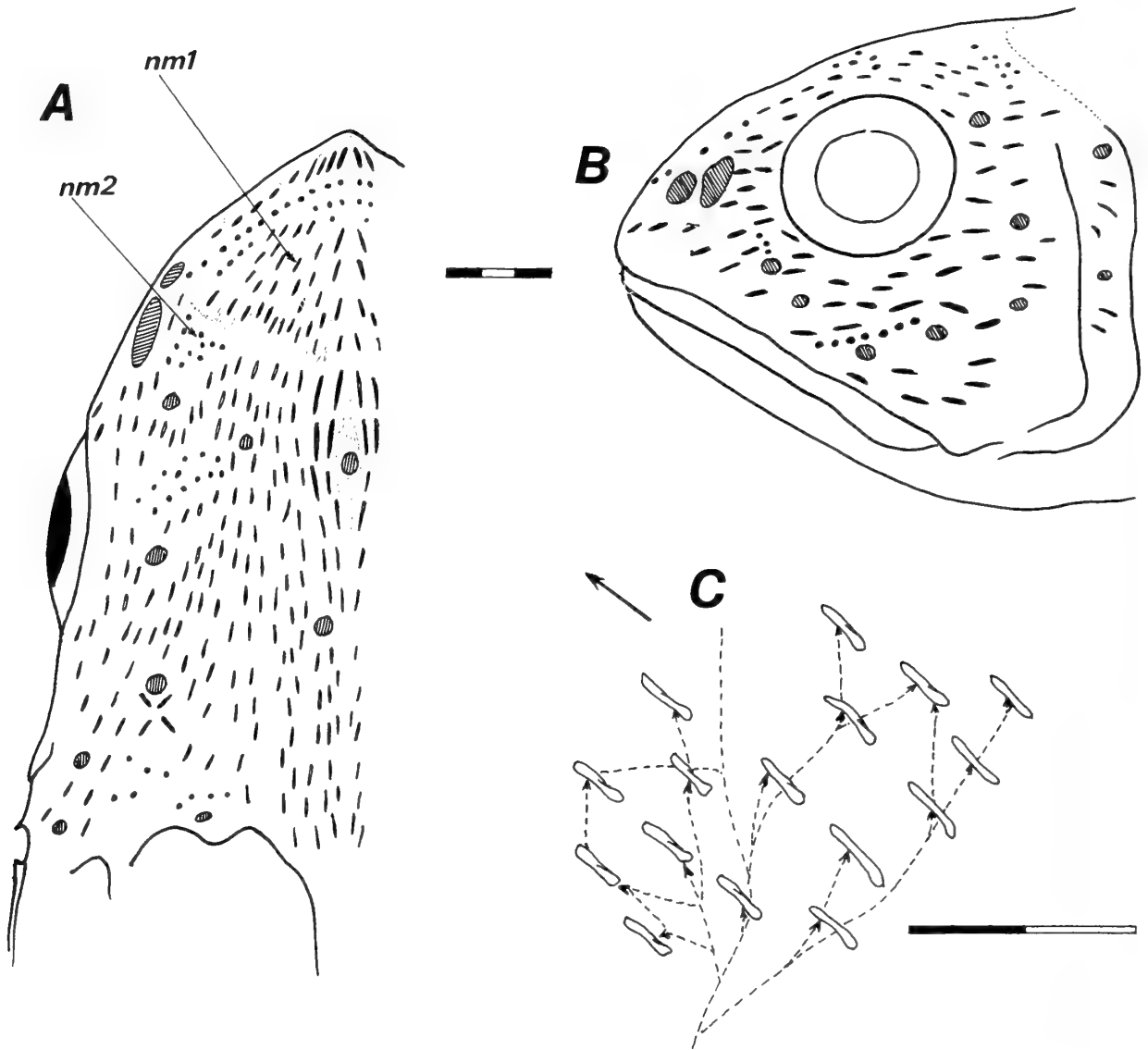


Fig. 2. Distribution of neuromasts types 1 and 2 in A, *Melanonus zugmayeri* on dorsal surface of head and B, *M. gracilis* on lateral surface of head. C, innervation pattern of type 1 neuromasts in subnasal region (right side) of *M. zugmayeri* (dashed lines indicate nerves, arrow heads indicate termination of nerve branch; large arrow points anteriorly). In this and subsequent figures, scale bars in millimetre divisions.

oblique row across the lower part of the cheek and a double row across the epioccipital region (Figs 2A,B). The neuromasts do not extend backwards on to the body.

There are about 500 flange-like neuromasts covering the entire head. Innervation is by the ramus canalis lateralis (Rc1 *sensu* Freihöfer, 1970) which exits from the posterior frontal foramen to anastomose through a loose fascia of connective tissue. The neuromasts are innervated by subbranches stemming from a complex nerve network (Fig. 2C).

The Rc1 nerve branches from the supraorbital trunk of the trigeminal complex, (Fig. 17), a condition similar to that in *Merluccius* (Freihöfer, 1970). The branch innervating the large posterior neuromasts enclosed in the frontal sensory canal detaches separately from the supraorbital trunk, whereas in *Merluccius* the nerves separate off together.

The large, plate-like neuromasts, housed in the sensory canals number two in the nasal bone, three in the frontal (one beneath the anterior medial ridge, one beneath the lateral arch and one posteriorly), one in the anterior part of the

pterotic, one in the parietal, one in each extrascapular, three in the first infraorbital, one in the second, third and fourth, two in the fifth and one in the sixth, and five in the preoperculum.

Infraorbitals (Fig. 3).

There are six infraorbital bones, the first long and relatively deep with a broadly fretted ventral border, the outer flange which forms the roof to the sensory canal extends as a shelf along the anterior half of the bone, but curves laterally along the posterior half. The ascending process which contacts the posterior wall of the lateral ethmoid is tall and spine-like. The second infraorbital is confluent with the first and is as deep but only a sixth of its length. The medial lamina of the third is widely separated from that of the second although the dorsolateral flange is nearly in contact. The third together with the fourth form the posteroventral corner of the orbit and the fourth has only a short orbital margin and flange

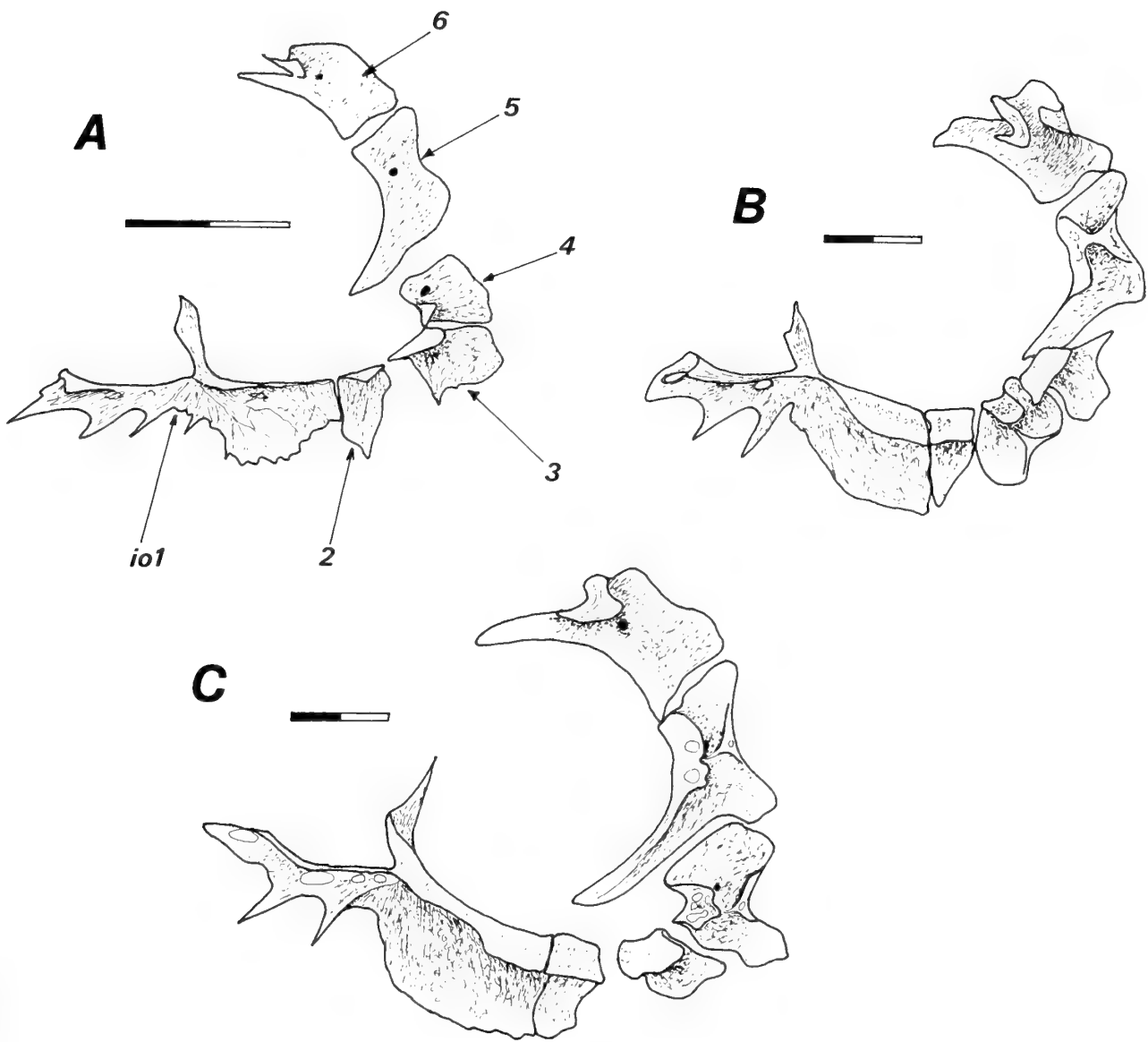


Fig. 3. Infraorbital bones of *M. zugmayeri* in specimens of: A, 66mm SL; B, 100mm SL and C, 130mm SL.

posteriorly, the body of the bone is expanded. The fifth infraorbital has a long orbital margin, the lower part of which projects anteroventrally in front of both the third and fourth to which it is connected by strong connective tissue; it has a narrow flange along its upper orbital border. The sixth (dermosphenotic) is as large as the fifth and has a pronounced orbital curvature which brings its anterior tip to the same vertical plane as the ascending process of the first infraorbital.

In the two smaller specimens of *M. zugmayeri* examined, the dorsolateral flange remains undeveloped on the first, fifth and sixth infraorbitals of the 66mm specimens and the ascending process of the first infraorbital is inclined anteriorly in both (Fig. 3A). The anteroventral border of the fifth infraorbital is less pronounced and in the 100mm SL specimen its tip lies medial to the rim of the fourth infraorbital; the sixth lacks the anterior elongation of the larger (130mm SL) specimen (Figs 3B, C).

Unlike other gadiforms where the posterior (fifth and sixth) infraorbitals are shallow, those of *Melanonus* are as deep as the anterior ones. The anterior curvature of the upper infraorbital (dermosphenotic) is more reminiscent of some macrouroids (see below) than gadoids. The central position of the ascending process of the first infraorbital is probably a plesiomorphic gadiform feature (on the basis of commonality) as is the reduced size of the second infraorbital. The extension of the lower part of the fifth infraorbital and the enlargement of the dermosphenotic are, because of their restricted distributions, taken to be derived features. According to Iwamoto (1989) among macrouroids, exclusion of the third and fourth infraorbitals from the orbit is a derived condition. In *Melanonus* similar exclusion has resulted from ventral extension of the fifth infraorbital whereas in the macrouroids illustrated by Iwamoto (1989, fig. 5G) it is due to re-alignment of the fourth infraorbital which covers the orbital borders of the second and third.

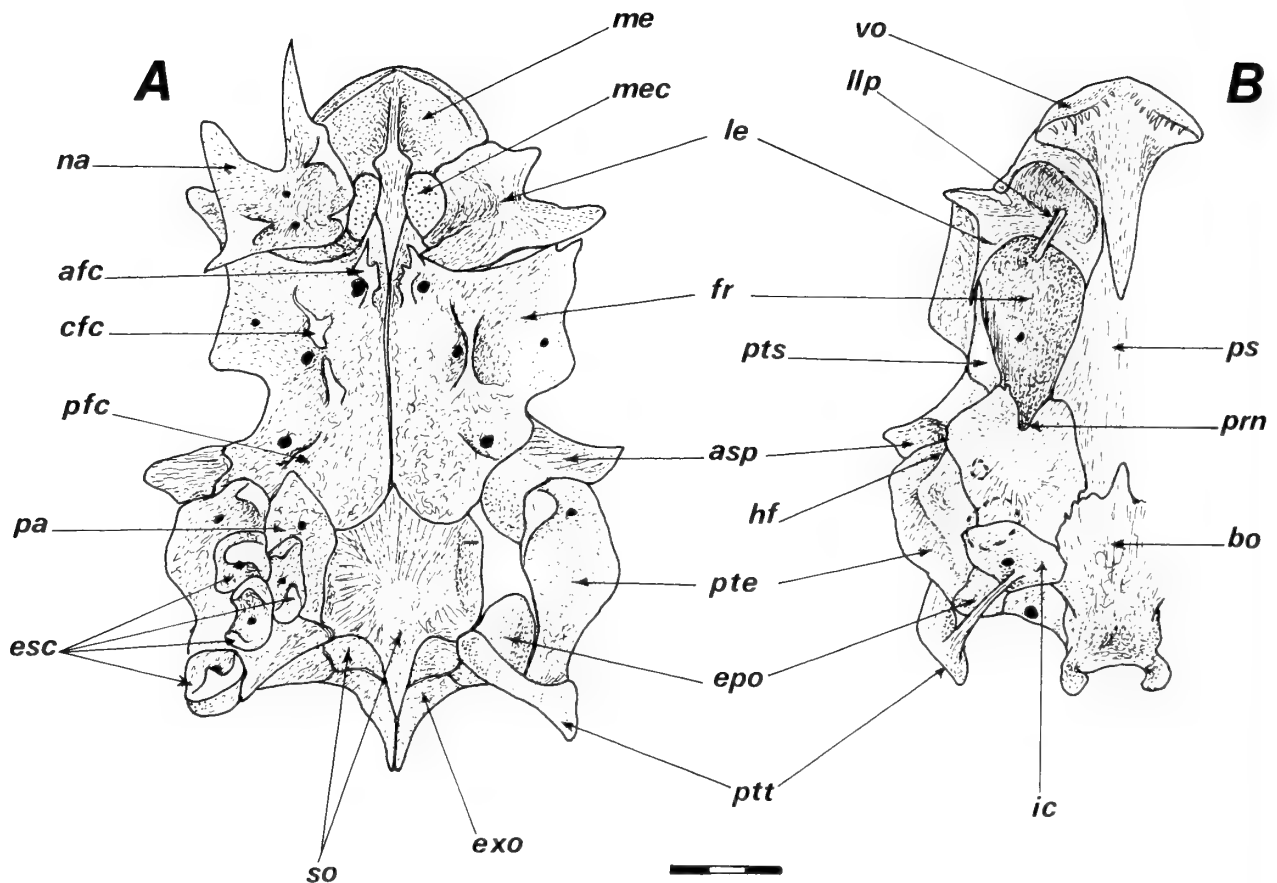


Fig. 4. Neurocranium of *M. zugmayeri* in A, dorsal and B, ventral views. In A, the right parietal, right nasal and left posttemporal have been removed. In B, dashed outline circles on the prootic and intercalar indicate the positions of the otoliths.

Cranium (Figs 4–8).

In its overall shape the cranial roof is almost square, the most noticeable feature being the deep indentation of the lateral frontal border anterior to the sphenotic, and the prominent anterolateral projections of the lateral ethmoid wings (Fig. 4A).

The *ethmoid* dorsal surface (rostrodermosupraethmoid) is, in keeping with that of other gadoids (Howes & Crimmen, 1990: 166), being narrow and cruciform with a steep anterior slope (Fig. 5B). The ossified anterior wall of the ethmoid forms most of the nasal cavity and a thin, vertical septum of ethmoid cartilage separates the cavities medially. A shallow bed of cartilage separates the base of the ethmoid and the vomer. The *vomer* has a thick, broadly rounded head bearing on either side 6 or 7 teeth in smaller specimens and 10–12 in larger (Figs 4B, 6A). In smaller specimens of both species the teeth are more or less arranged in a single row but in larger specimens the posterior teeth tend to be in a patch with one or two stout and caniniform being almost twice the length of their neighbouring teeth and three times that of the symphyseal teeth (Fig. 6A). The vomerine shaft is relatively short, extending to just beyond the posterior level of the lateral ethmoid. The base of the *lateral ethmoid* is long and broad and where it meets the vomer bears a deep cavity into which inserts the palatine ligament. The wall of the lateral ethmoid is thin and projects forward at an angle of 45°. The postero-

medial wall extends backward to directly contact the pterosphenoid.

The *nasals* (Fig. 4A) are large, almost entirely covering the lateral ethmoid and are narrowly separated from one another in the midline by the rostrodermosupraethmoid. Each bone has prominent anterior and posterolateral processes, two dorsal processes, lateral and medial, are folded inward to form curved flanges which support the skin roofing the sensory canal. In large specimens the nasals tend to become narrow with attrition of the anterior process (Fig. 6B).

The *frontals* are nearly square except that the posterior half of the lateral border is deeply indented. Anteriorly, close to the midline is a high, arch-shaped crest (afc, Fig. 4A), a similar but longer arch is situated in the centre of the bone and is sometimes divided into two separate crests (cfc, Figs 4A, 5B), posteriorly is a low, diagonal crest (pfc, Fig. 4A). All these crests shelter a neuromast foramen and serve to support the skin covering the frontal canal system. Posteriorly, the frontal margin meets the pterotic, is overlapped by the parietal and partially overlaps the anterior border of the supraoccipital. There are no ventral frontal laminae. The *parietals* (Figs 4A, 5B) are thin, near-diamond shaped bones each with a single neuromast foramen and posterolaterally covered by the median extrascapular. There is no parietal crest.

The *autosphenotic* (Figs 4A,B, 5B) has a prominent, bluntly rounded lateral process and is overlapped by the

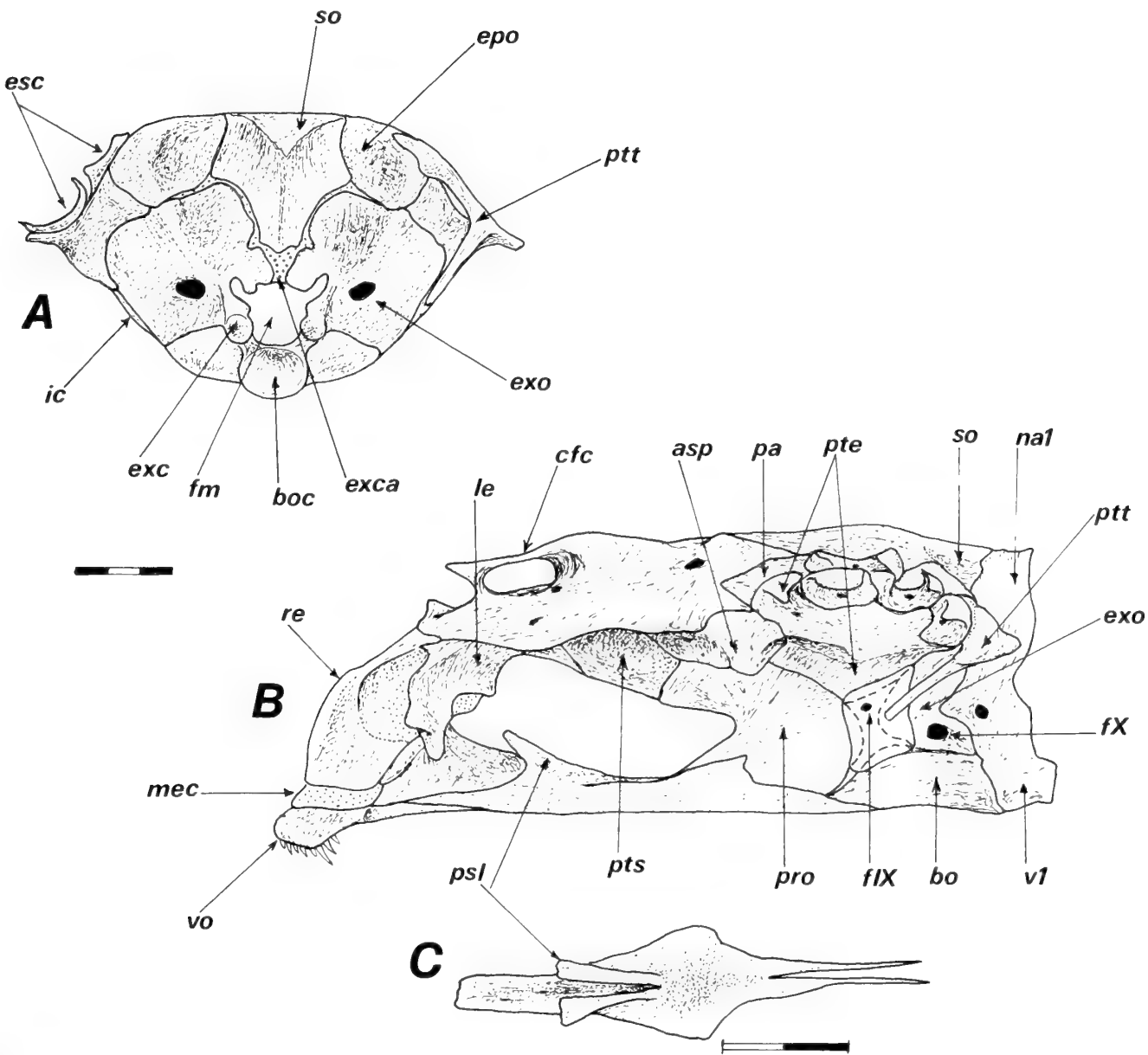


Fig. 5. Neurocranium of *M. zugmayeri* in A, posterior and B, lateral views. In B, the intercalar is unshaded, the margins of the bones underlying it indicated by dashed lines. C, parasphenoid of 66mm SL specimen in dorsal view.

frontal, parietal and pterotic. The underside of the bone bears a deep, almost transverse fossa into which articulates the hyomandibular. The *pterotic* (Figs 4A,B, 5A,B) accommodates the posterior portion of the hyomandibular fossa along a third of its lateral border. The wall of the pterotic is somewhat bullate and its cranial surface forms a prominent lateral shelf.

The *pterosphenoid* (Figs 4B, 5B) is long and deep forming most of the dorsomedial wall of the orbit, anteriorly it contacts the frontal and posteriorly the autosphenotic and prootic. The *parasphenoid* (Figs 4B, 5B,C) has a broad keel with, extending from its centre, a long, low ascending process which extends laterally at a low angle to the horizontal plane to meet the prootic; paired, parallel laminae rise from the central region of the keel to meet the bases of the lateral ethmoid wing (Fig. 6).

The *prootics* (Figs 4B, 5B) are large with a deep trigeminal notch. The posterior border of the bone is rounded and partially overlapped by a relatively small, ovoid *intercalar* to which is attached the inferior limb of the posttemporal (Figs 4B, 5A,B, 6D). The small, pinnacle-like *epioccipitals* contact the posterolateral margins of the supraoccipital and posteriorly the dorsal borders of their respective exoccipitals; laterally each epioccipital is overlain by the second extrascapular (Fig. 4A).

The *exoccipitals* are deeply depressed posteriorly and contain a large, backwardly facing vagus foramen (Figs 5A,B, 7). Medially, the bones meet across the midline by flange-like projections. Posteriorly there is an ovate, cartilage-filled process the base of which meets its antimeres in the midline. Inside each exoccipital a long, ventrally directed process extends from the medial surface to contact a shallow dorsal

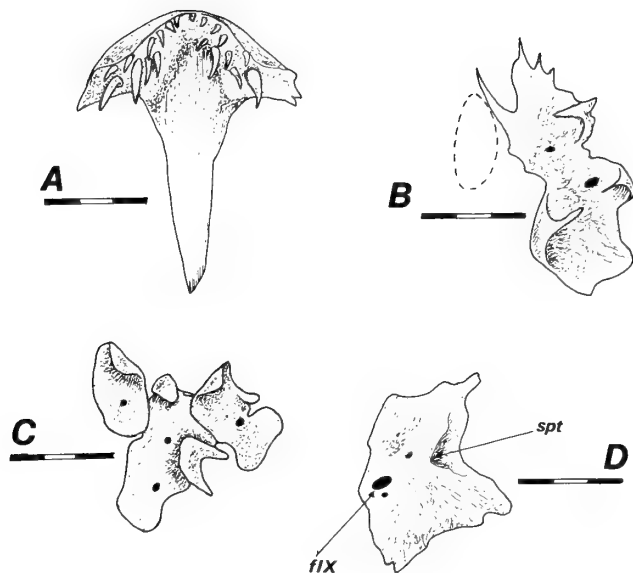


Fig. 6. *Melanonus zugmayeri*: A, vomer in ventral view; B, nasal of left side in dorsal view (broken outline indicates anterior nasal opening); C, extrascapulars of left side in lateral view; D, intercalar (left, lateral view). All from a specimen of 173mm SL.

flange rising from the base of the basioccipital (Fig. 7B). The *basioccipital* is a trowel-shaped bone the blade of which forms the posterior basicranium and the handle, the occipital condyle (Figs 4,5,7). The *supraoccipital* (Figs 4A, 5A,B, 7) is well-ossified and lies flush with the frontals, its crest confined to its posterior margin; laterally, the bone is bevelled where it meets the parietal. Posteriorly its ventral margin is bordered by the exoccipital.

The *otoliths* have been described and figured by Nolf & Steurbaut (1983; 1989).

Comments on cranial features

Melanonus has a plesiomorphic ethmo-vomerine region, namely a broadly rounded ethmoid lacking any dorsal elevation as in macrouroids and with a single, narrow point of contact with the lateral ethmoid (Howes & Crimmen, 1990; a more extensive area of contact appears to be a feature of some supragadoids, Howes, 1990); a laterally expanded lateral ethmoid which contacts the ascending process of the first infraorbital ligamentously on its posterior face (Howes, 1987); vomer with a relatively short shaft and well-formed teeth (absence of vomerine teeth in Macrouroidei and some gadoids is considered independently derived; see Okamura, 1989; Inada, 1989; Howes, 1990). Ophidiiforms have as broad a variability of the ethmovomerine region as gadiforms but the lateral ethmoid is characterised by the presence of basal twin facets which firmly unite with the large palatine head. Furthermore, the lateral wing of the lateral ethmoid is usually reduced and feebly developed, but always has a lateral facet which articulates with the first infraorbital (Howes, 1992).

The frontals of *Melanonus* have a plesiomorphic gadiform morphology; both gadoid and macrouroid taxa bear frontal crests of varying development as do ophidiiforms and this

may be a 'paracanthopterygian' feature. Howes (1990:79) noted the lack of ventral frontal laminae in *Melanonus* and considered this a derived condition associated with the anterior displacement of the frontal area of the brain (see p.27). Ventral frontal laminae are widely distributed amongst ophidiiforms. There is no prominent V-shaped ridge pattern on the frontals in *Melanonus* and no 'mucosal' cavity, a feature of supragadoids.

Nasal bones are plesiomorphically separated in the midline but in macrouroids are joined for most of their lengths, a feature regarded as synapomorphic for the group (Iwamoto, 1989; Howes & Crimmen, 1990). Among gadiforms the size of the nasals is variable but they are nearly always large, trough-like bones containing two neuromasts. Among plesiomorphic gadoids (e.g. Bathygadidae) the size of the nasals approaches that of macrouroids but the bones remain separated along the midline. The melanonid condition is thus considered plesiomorphic although the nasal bones have a distinct apomorphic shape which more closely approaches that of some macrouroids than gadoids.

The pterotic of *Melanonus* has a plesiomorphic gadiform morphology and resembles that of Bathygadidae in being broad with a rounded posterior margin and short hyomandibular fossa (Howes & Crimmen, 1990, fig. 6).

The pterosphenoid is unusually large for a gadiform; the widespread condition (and among ophidiiforms) being small, occupying the dorsoposterior region of the orbit and widely separated from the lateral ethmoid. The enlarged anteriorly extended bone is therefore considered autapomorphic for *Melanonus*. The parasphenoid displays no particular derived feature and corresponds with the situation in the majority of gadiforms, namely a broad flat keel with parallel laminae (Howes, 1990:81).

The deeply incised trigeminal notch of the prootic resembles most closely that of some Phycidae and the Muraenolepididae, but unlike those taxa the anterior wall of the prootic is directed medially as in most infragadoids and macrouroids (Howes, 1990:82). The intercalar is small in comparison with that in other gadiforms where in gadoids it is exceptionally large covering the entire posterolateral cranial wall. A large intercalar is one of the characters diagnostic of paracanthopterygians but is secondarily absent in lophiiforms and batrachoidiiforms. Among ophidiiforms and percopsiforms the intercalar is generally not as large as that of gadiforms, and in those two former groups is confined to the upper half of the posterior cranial wall and does not extend ventral to the basioccipital anteriorly but is interrupted by the prootic.

The relationship between the epioccipital and supraoccipital is an unusual one amongst gadiforms in that the posterior walls of the exoccipitals meet across the midline and so exclude the supraoccipital from contributing to the upper margin of the foramen magnum. Elsewhere in paracanthopterygians this condition occurs among ophidiiforms (Howes, 1992) where the exoccipital has enlarged backward and upward to cover the posterior margin of the supraoccipital. Even in the largest cleared and stained specimen of *M. zugmayeri* examined for this feature the ventral tip of the supraoccipital does not reach the margin of the foramen magnum (Fig. 7B). The supraoccipital lacks a dorsal crest, there being a posterior lamina (Fig. 7). Howes (1990:82) discussed the variability of the supraoccipital crest amongst gadoids. An elevated cranial crest is possibly the plesiomorphic condition for paracanthopterygians but a low, reduced crest is widely distributed amongst all groups and in lophii-

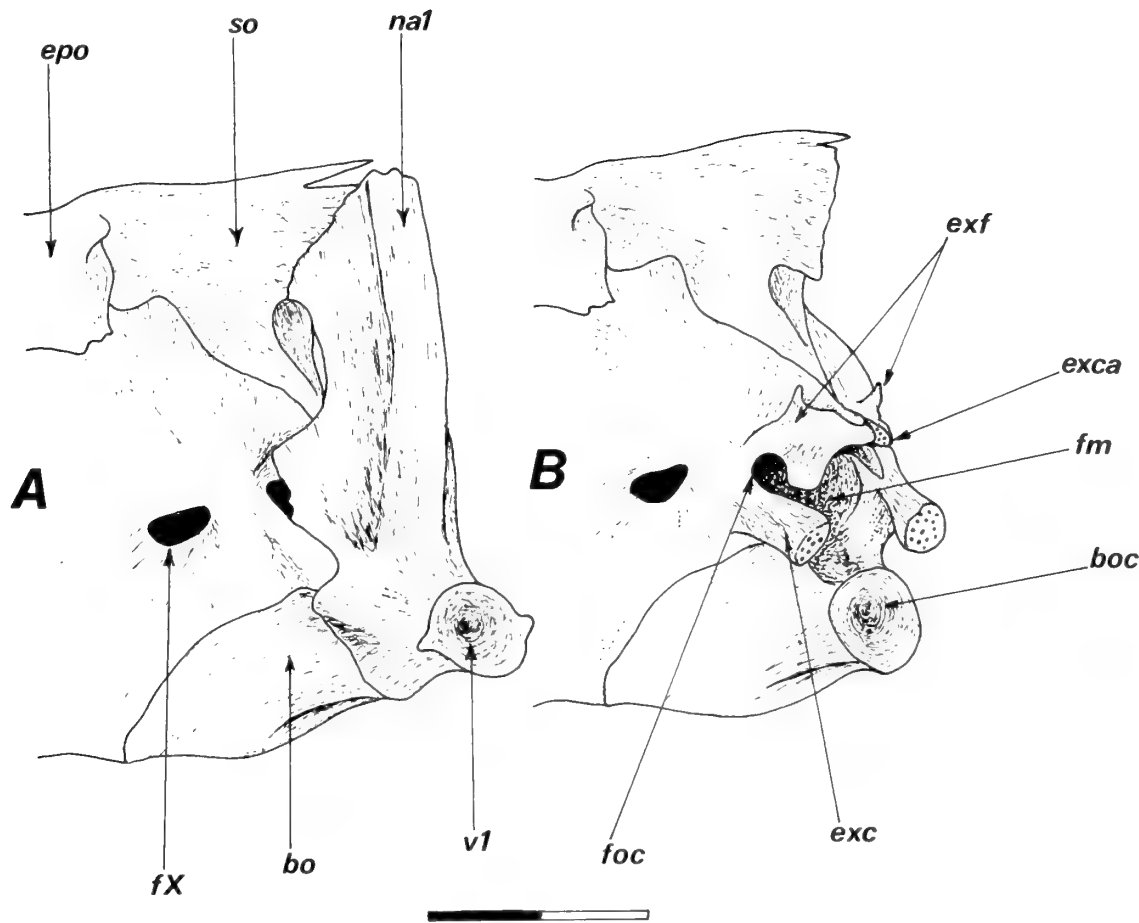


Fig. 7. *Melanonus zugmayeri* posterior part of cranium in lateral oblique view of 130mm SL specimen showing in A, first neural arch and vertebra attached and in B, removed to expose the posterior features of the basi- and exoccipitals. Note the supraoccipital does not contribute to the border of the foramen magnum.

forms and ophidiiforms appears to be the common condition. It is assumed that this feature has been repetitively evolved in these groups.

Jaws (Fig. 8)

The *premaxilla* (Fig. 8C) has tall, thin and widely separated ascending and articular processes, and a tall, spine-like postmaxillary process. The toothed surface is narrow, bearing for most of its length two rows of sharp pointed teeth. The outer row teeth are straight or extend slightly laterad, the inner row teeth which are about twice the length of the outer are inwardly curved; posteriorly there are three rows of teeth, the ones of the centre row being the same size as those of the inner (Figs 8D,E). In a 100mm SL specimen of *M. zugmayeri* the posterior teeth are so arranged as to form distinct transverse rows (Fig. 8F) but this is not evident in the 66mm or 130mm SL specimens. The *maxilla* has a tall articular head and a short medial articular process forming a rather acute angle with the head (Figs 8A,B). The shaft of the bone is slender and posteriorly bears shallow dorsal and ventral processes.

The *dentary* (Fig. 8G) is short and deep with a corresponding shallow mentomeckelian cavity; it has a high steep coronoid process. The sharp pointed teeth are set in an

irregular single row, numbering 22 in 88mm and 100mm SL specimens of *M. zugmayeri*, 28 in a 130mm and 34 in a 175mm SL specimen. The anterior teeth are small followed by four or five successively larger ones, then four or five relatively large teeth separated by three or four smaller ones. Posteriorly the teeth diminish in size. The *anguloarticular* (Fig. 8G) is tall with a steep posterior slope and short, vertical anterior margin; the articular condyle is long and narrow. The *coronomeckelian bone* (Fig. 8G) is a well-developed, cylindrical element with slight dorsal and ventral posterior flanges. The *retroarticular* (Fig. 8G) is boot-shaped, the leg being curved forward and the foot long and shallow. A strong labial ligament is anchored to the rim of the dentary (Howes, 1988, fig. 12).

The overall jaw morphology of *Melanonus* is plesiomorphic for gadiforms, the upper jaw bones, apart from having a smaller postmaxillary process of the premaxilla, are little different from those in bathygadids (Howes & Crimmen, 1990). Macrouroids are characterised by having a large postmaxillary process of the premaxilla situated posteriorly (Okamura, 1970; Howes & Crimmen, 1990). There is no 'gadoid notch' at the base of the postmaxillary process. The lower jaw more closely resembles that of gadoids or ophidiiforms than macrouroids in having a relatively shallow anguloarticular and boot-shaped or J-shaped retroarticular.

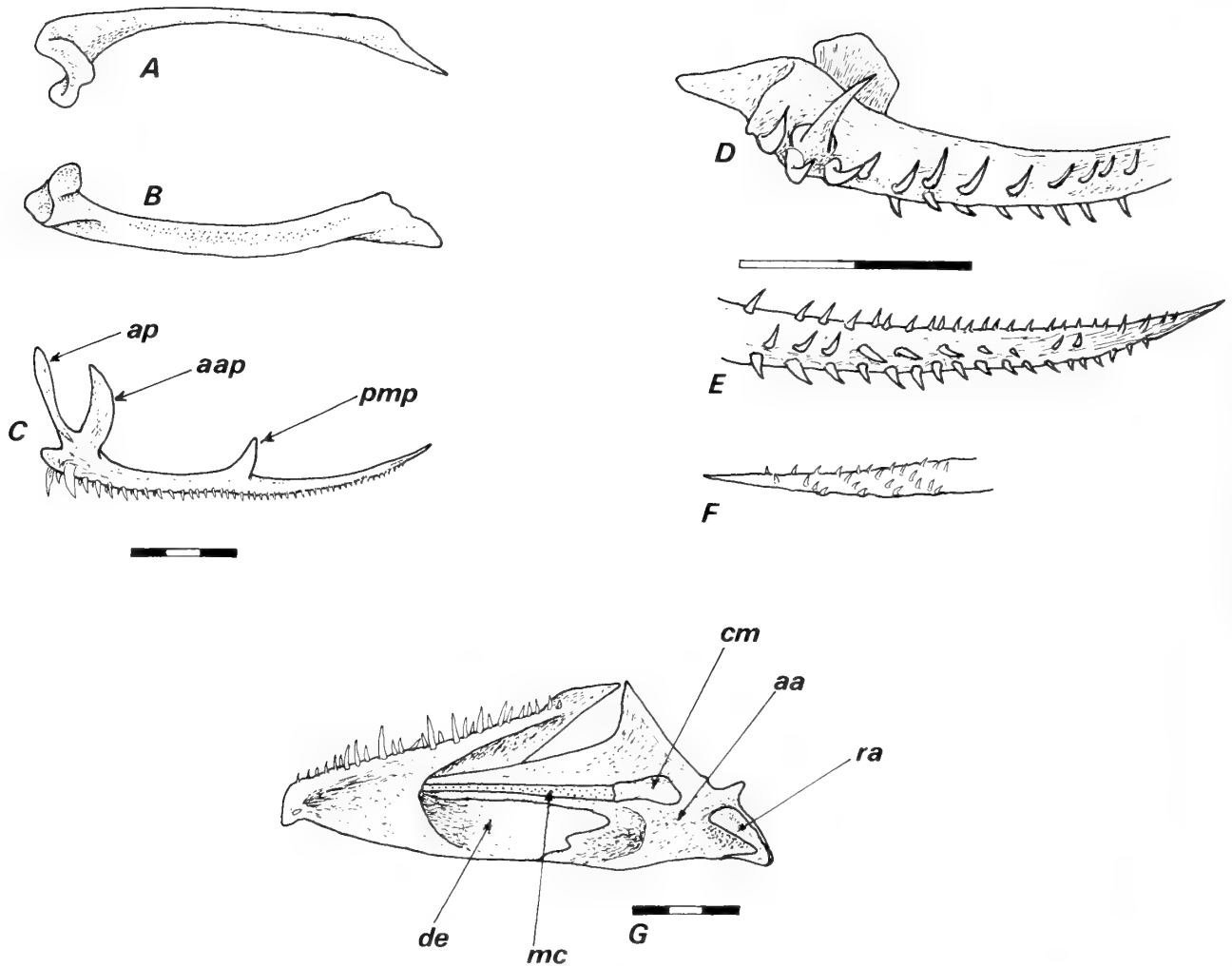


Fig. 8. *Melanonus zugmayeri*, jaw bones. A and B right maxilla from a 130mm SL specimen in: (A) dorsal and (B) medial and slightly ventral views; C, premaxilla in lateral view; D–F premaxilla, anterior (D) and posterior (E) regions from 130mm SL specimen and (F) 100mm SL specimen, ventral views; G, lower jaw of 130mm SL specimen in medial view.

Macrouroids tend toward a deeper anguloarticular and greater variability in the shape of the retroarticular (Okamura, 1970; Howes & Crimmen, 1990). A boot-shaped retroarticular is lacking in both percopsiforms and lophiiforms.

Palatopterygoquadrate (Fig. 9)

The *palatine* (Fig. 9A,B) is long, its posterior tip extending to nearly halfway along the ectopterygoid, its rostral process is long and slender and overlies the maxilla, its base bears a broad facet which articulates with the ethmoid cavity and the body of the bone rises to a high posterior crest. There are two rows of sharply pointed teeth.

The anterior part of the *ectopterygoid* (Fig. 9A) lies along the medial face of the palatine and its ventral stem reaches the quadrate joint; laterally it is slightly overlapped by the *entopterygoid* (Fig. 9A). The latter is a relatively large bone with a rounded dorsal profile and is sloped mesad, its posterior border is well separated from the hyomandibular by the *metapterygoid*. The *metapterygoid* (Fig. 9A) is axe-shaped its posterior margin rising high up the leading edge of the hyomandibular shaft.

The melanonid palatine is unique amongst gadiforms, in its length, nature of contact with the pterygoids, and in bearing teeth. The common condition, and one which is considered synapomorphic for gadiforms (p.29) is for the palatine to be reduced in length with a vertical or slightly angled posterior border meeting a similar blunt margin of the ectopterygoid and forming a hinge-type joint (see figures in Okamura, 1970, 1989; Howes, 1990, 1991b; Howes & Crimmen, 1990). This union differs from that commonly encountered in other paracanthopterygians where the posterior limb of the palatine is attenuated and articulates firmly with the leading edge of the entopterygoid and lateral face of the ectopterygoid. Percopsids resemble gadiforms in having a near vertical abutment of the palatine with the ento- and ectopterygoids (Fig. 9D). However, there is a posterior stem which overlaps the upper lateral margin of the ectopterygoid. Macrouroids are characterised by the lack of direct contact between the palatine and ethmovomerine bloc (Howes & Crimmen, 1990).

Norman (1930) noted there were 'teeth on the pterygoid', an error perpetuated by Howes (1991b, caption to fig. 35). The pterygoid bones of *Melanonus* display plesiomorphic morphologies; the large entopterygoid and high posterior

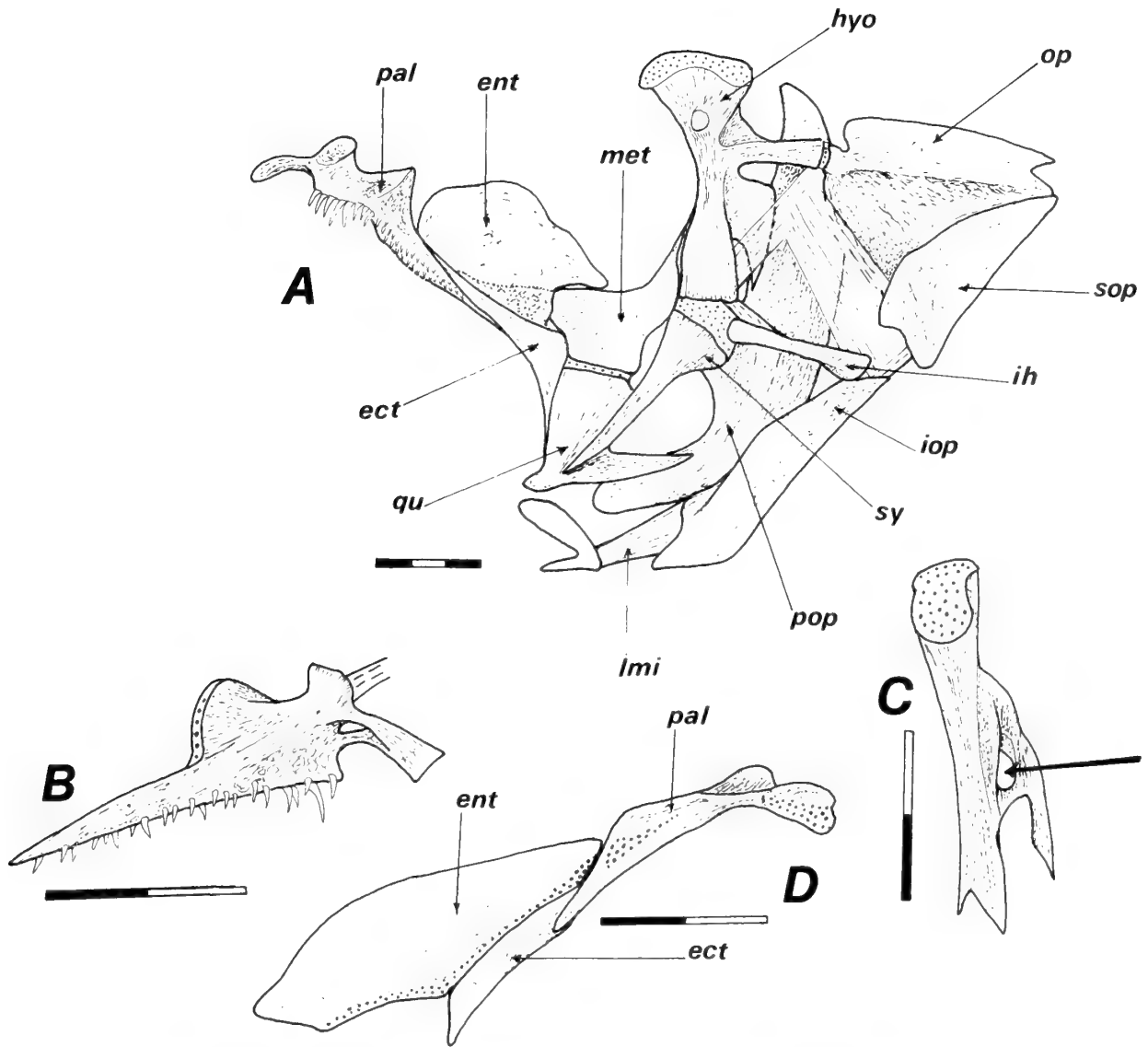


Fig. 9. A–C *Melanonus zugmayeri*: A, palatoquadrate, hyosymplectic and opercular bones of 130mm specimen in medial view, light hatched area represents ligamentous system connecting opercular bones to hyomandibular; B, palatine of 100mm specimen, right side, lateral view; C, hyomandibular, left side, of 100mm SL specimen in anterior view showing foramen for hyoid branch of facial nerve (arrowed) and lateral flange; D, *Percopsis omiscomayus*, palatine and pterygoids in lateral view (heavy dotting indicates cartilage).

metapterygoid process are present in macrouroids, bathygadids and macruronids (Howes & Crimmen, 1990; Howes, 1991b). Reduction of the entopterygoid and metapterygoid appears to be characteristic of supragadoids (Howes, 1990). Amongst ophidiiforms the metapterygoid abuts against the lower limb of the extended anterior portion of the hyomandibular.

The quadrate (Fig. 9A) of *Melanonus* has a wide angle between its posterior border and the posteroventral spine. The size of this angle is variable among gadiforms and appears correlated with the orientation of the suspensorium. An 'interosseous space' between the symplectic and preoperculum (Okamura, 1970; 1989) is also a condition of the angular separation of the two parts of the quadrate, being absent where the angle is small (Howes, 1990).

Hyoid arch (Figs. 9–11)

The hyomandibular (Fig. 9A) has, as in all gadiforms, a single articulatory condyle. The bone is narrow-waisted with the relatively long shaft oval in section, a foramen for the hyoid branch of the facial nerve pierces its posterior margin (Fig. 9C). Posteriorly is a long, horizontal process which articulates with the opercle. The lateroposterior face contacts the border of the preopercle. Medially a band of ligamentous connective tissue joins the shaft with the opercular process and a wider band runs at right angles to it to attach to the subopercle and interopercular-subopercular ligament (Fig. 9A).

The course of the hyoid branch of the facial nerve is partially exposed laterally, due to attrition of the outer part of the hyomandibular, part of which remains as a lateral flange which is a common feature (synapomorph) for gadiforms,

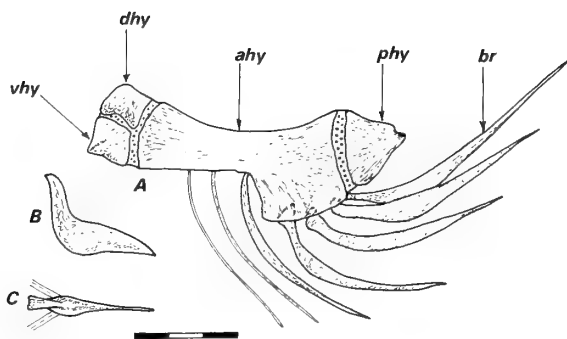


Fig. 10. *Melanonus zugmayeri* hyoid bar of 100mm SL specimen: A, medial view; B and C, urohyal in lateral and dorsal views.

one not shared by ophidiiforms or lophiiforms (Howes, 1992).

Other hyoid arch bones are much like those of the majority of gadiforms; the posterior half of the *anterohyal* = *ceratohyal auct.* (Figs 10A, 11A) is deep and in this respect resembles that bone in some macrouroids (eg. *Nezumia*, *Abyssicola*, *Coelorhynchus*, *Coryphaenoides*; Okamura, 1970), more closely than gadoids. However, this feature is variable and a similar range of morphotypes can be found among ophidiiforms (Markle & Olney, 1990, fig. 13). As in most gadiforms and ophidiiforms there are 7 *branchiostegal rays* which appears to be the plesiomorphic paracanthopterygian number, (six occur frequently in lophiiforms). The *urohyal* (Figs 10B,C) bears a closer resemblance to that of gadoids rather than macrouroids in having a shallow dorsal keel and a long, prominent anterodorsal (basibranchial) process (Howes, 1990, fig. 16B).

The *basihyal* (Fig. 11A) is a dumbbell-shaped bone lying between the dorsohyals and crossed by a ligament which connects them; anteriorly a thick cartilaginous 'tongue' protrudes forward, posteriorly, the basihyal is slightly overlapped by the first basibranchial (see below). The *interhyal* (Fig. 9A) is typically gadiform, being long and slender, contacting the symplectic cartilage dorsally and the posterior socket of the posterohyal ventrally. Markle (1989, fig. 6A) shows a common ligamentous connection between the interhyal-posterohyal and interopercle. I find this to be one involving thick connective tissue although a discrete ligament runs from the medial side of the interhyal to the medial posterior tip of the posterohyal.

Opercular bones (Fig. 9A)

The opercular bones are relatively generalised except that the suboperculum has a straight to concave leading edge rather than the common gadiform condition of a rounded to pointed margin. The *interopercle* is shallow and nearly oblong with rounded dorsoposterior and anteroventral borders; it is widely separated from, and ligamentously connected to the subopercle. In general, macrouroids have the interopercle orientated horizontally (e.g. Okamura, 1970, figs 26; 27) whereas in gadoids the bone is angled, sometimes steeply as in *Melanonus*. *Melanonus* lacks the interopercular fossa present in a subgroup of 'supragadoids' (Howes, 1990). The *opercle* is relatively large for a gadiform and overlaps most of the subopercle. The *preopercle* has a short lower, anteriorly directed limb and a narrow laminate (symplectic) process

which, plesiomorphically, contacts the symplectic cartilage. In its derived form the symplectic process of the preopercle contacts the lateral face of the hyomandibular (Howes, 1990).

Branchial arches (Fig. 11)

There are three *basibranchials* (Fig. 11A), the first and second ossified, the third cartilaginous. The posterior margin of the first overlies the the anterior border of the diamond-shaped second which is separated from the small diamond-shaped third. The first and second *hypobranchials* (Fig. 11A) are long with marked posterior curvature, both contacting the first basibranchial and bear gill-rakers on their outer and inner margins; the third is short and lacks gill-rakers. The first and second *ceratobranchials* (Fig. 11A) bear five or six clustered-spinous rakers on their outer and the same number of slender, triple-spine rakers on their inner margins; the third has seven outer and inner shorter rakers and the fourth has four short rakers on its outer margin only. The anterior tips of the fifth ceratobranchials are apposed but not firmly united in the midline and are ligamentously connected to the third basibranchial; a narrow tooth patch bears *ca* 25 slender pointed teeth.

The *epibranchials* (Fig. 11B) are 30% the length of the ceratobranchials. A strong uncinate process on the first epibranchial is connected by a chondrified ligament to a large interarcual cartilage; the third epibranchial bears a long tooth plate bearing *ca* 20 sharp pointed teeth. There are four *pharyngobranchials* (Fig. 11B), the first being an ossified element; the second-third pharyngobranchial tooth plates bear strong, pointed teeth.

Markle (1989) has described and commented on the upper

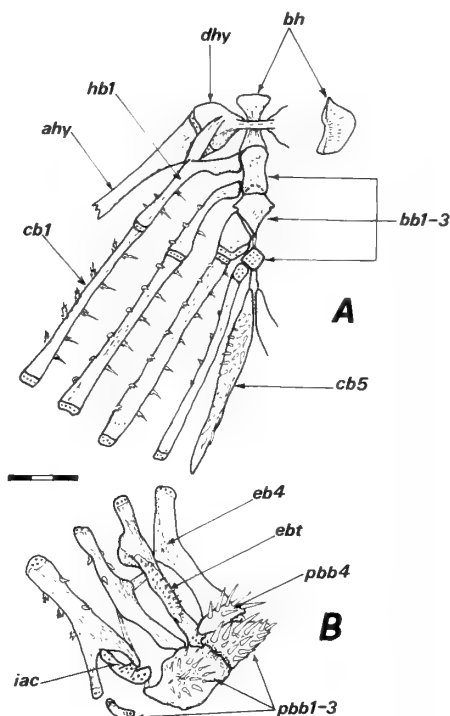


Fig. 11. *Melanonus zugmayeri* branchial arches of 130mm SL specimen: A, dorsal view of lower arch elements; B, ventral view of upper arch elements. In A, basihyal is also shown in lateral view.

branchial arch of *Melanonus* which he considers, due to the presence of a large and chondrified interarcual ligament, to be plesiomorphic for gadiforms. In his cladogram, however, he mistakenly ascribes to *Melanonus* the loss of the second pharyngobranchial. The lower gill-arch is also plesiomorphic in that the basibranchials are unexpanded and there is no forward ventral elongation of the third hypobranchial as in macrouroids and ophidiiforms; the first hypobranchial is typically long as in gadiforms but lacks an expansion where the ligament running to the dorsohyal attaches. Spinous gill-rakers of both the clustered- and triple-spine type are widespread amongst 'infragadoids' and macrouroids.

Pectoral girdle (Fig. 12)

The vertical and horizontal limbs of the *cleithrum* (Fig. 12A) are nearly equal in length; the medial cleithral lamina is thin and only prominent near the cleithral tip. Markle (1989) noted that the foramen which notches medial borders of both the scapula and coracoid is present only in the former (Fig. 12A). Markle (1989) and Howes & Crimmen (1990) commented on the variability of this feature; plesiomorphically the foramen lies entirely within the scapula, a condition

almost entirely confined to 'infragadoids' although it is also recorded in the 'supragadoid' *Lota*. The *supracleithrum* (Fig. 12B) is a lanceolate bone with a slightly expanded dorsal articular surface which contacts the posttemporal. There are four *actinosts* and 12 or 13 pectoral rays in the *M. zugmayeri* specimens examined (Norman, 1930, gives 13 for *M. zugmayeri* and 12–14 for *M. gracilis*; Fahay & Markle, 1984, give a range for the genus of 10–16). The single *postcleithrum* (Fig. 12A) has a broad head and slender, slightly upwardly curved stem. It articulates in a cleft opposite or slightly above the coracoid-scapula junction (see also Markle, 1989, fig. 10).

The *posttemporal* (Fig. 12B) is V-shaped, its upper limb broad proximally and tapering distally; its lower limb, which is firmly united with the intercalar is thin, rod-like and completely ossified.

The *extrascapulars* (Figs 4A, 5A,B, 6C) number four, each having upturned borders and containing a neuromast. The lateral extrascapular covers the posterior corner of the pterotic, two lie in contact with one another along the medial part of that bone and the innermost lies along the lateral part of the parietal. In large specimens of *M. zugmayeri* the

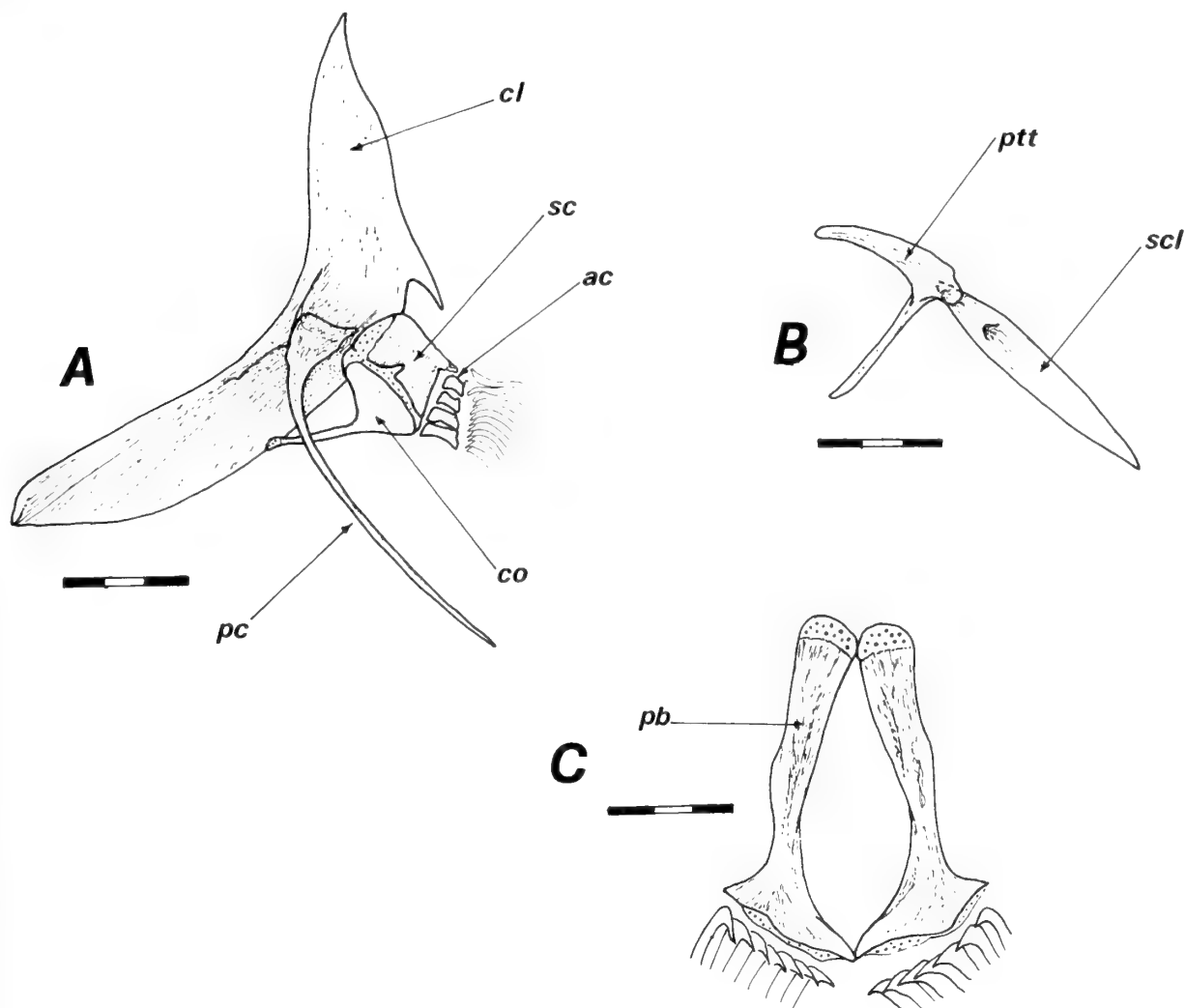


Fig. 12. *Melanonus zugmayeri*: A, pectoral girdle in medial view; B, posttemporal and supracleithrum in lateral views; C, pelvic girdle in dorsal view.

medial extrascapular is more closely aligned with the supraoccipital, resting along a lateral ridge of the bone and in a specimen of 173mm SL (Fig. 6C), it appears that the lateral and a medial extrascapular have become fused, judging by the presence of two neuromast foramina in the single large bone.

Pelvic girdle (Fig. 12C)

The pelvic bone is narrow and tubular, broadening proximally where its cartilaginous tip contacts its antimeric symphysially. Distally the pelvic process is narrow and straight and connected with its antimeric by ligamentous tissue. There is no lateral pelvic process or spine (cf. Bathygadidae, Howes & Crimmen, 1990). There are usually 7 fin rays; Fahay & Markle (1984) give a range for the genus of 5–7.

The pelvic girdle lies well forward with the anterior tips of

the pelvic bones lying between the cleithra so that the origin of the pelvic fin lies beneath or just anterior to that of the pectoral (Fig. 1). The position of the pelvic girdle in relation to the pectoral girdle is variable amongst gadiforms. In the majority of gadoids the pelvic girdle is situated well forward, particularly so in the more derived 'supragadoid' taxa such as gadids, gaidropsarids and muraenolepidids, so that the origin of the pelvic fin lies in advance of that of the pectoral fin. 'Infragadoids' tend to have the pelvic girdle situated beneath or behind the pectoral (e.g. bathygadids, steindachneriids). In morids, however, the pelvic girdle lies well forward. There is some variability in position among macrouroids but generally, the pelvic girdle lies posterior to the pectoral so that the origin of the pelvic fin is situated directly beneath that of the pectoral fin. With respect to the position of the pelvic fin relative to that of the pectoral, the Melanonidae appear to represent an intermediate condition between the derived forward and plesiomorphic posterior positions.

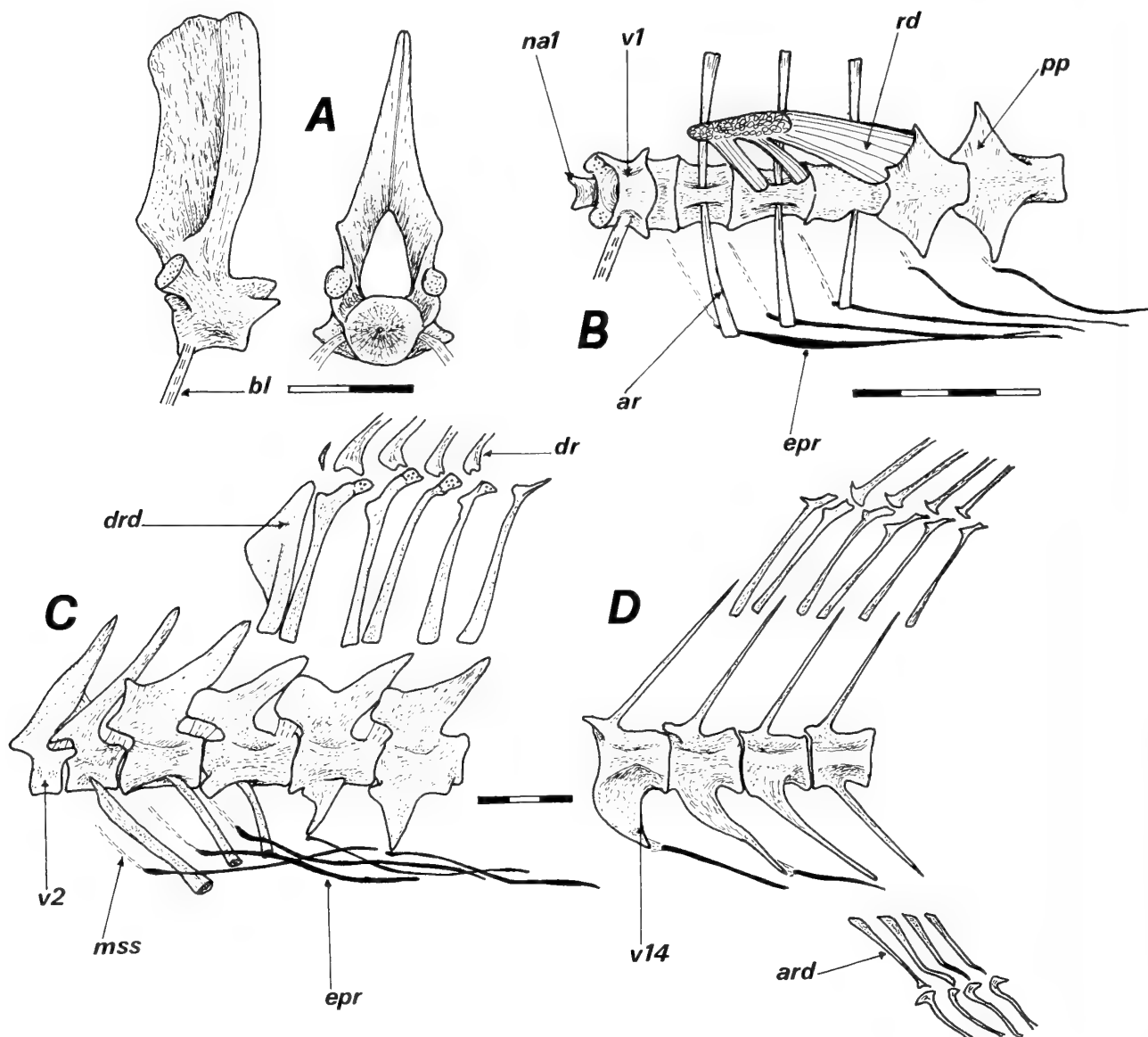


Fig. 13. *Melanonus zugmayeri* vertebral column. A, first vertebra and neural arch of 130mm SL specimen in lateral and anterior views; B, anterior part of vertebral column of 100mm SL specimen showing retractor dorsalis muscle of one side, in ventral view; C and D vertebral column and fin supports of 130mm SL specimen: C, anterior vertebrae, D, 14th-17th vertebrae showing anterior anal fin supports (lateral views; ribs shown in black for clarity).

Vertebral column and median fins (Figs 13–15)

There are 12–14 abdominal and 45 or 46 caudal (those with closed haemal spines) vertebrae in *Melanonus* (Fahay & Markle, 1984 give total counts of 58–62 for the genus). The first neural arch and spine are well-developed and form an ankylosed unit with the centrum. The prezygapophyses of the first vertebra (Fig. 13A) are oval in section, hollow and cartilage-filled and firmly in contact with the similarly shaped paired condyles of the exoccipital. The wall of the neural arch covers the upper posterior wall of the exoccipital leaving exposed a notch through which pass the occipital and lateral line nerves (Fig. 7B). The laminae of the neural arch extend forward to embrace the posterior extension of the supraoccipital crest (Fig. 7A). The second vertebra is anteroposteriorly compressed and lacks processes or ribs; the third-fifth vertebrae support successively shorter chopstick-shaped ribs which extend almost horizontally, at their tips lie epipleural (epineural) ribs the heads of which are ligamentously attached to their respective myosepta (Fig. 13B,C). The sixth-twelfth centra bear triangular parapophyses to each of which is attached a posteriorly curved epipleural rib. According to Okamura (1989) there is a total of eleven epipleural ribs in *Melanonus*; ten are counted here in *M. zugmayeri*.

There is a single dorsal fin comprising 72–78 rays. The first dorsal ray is often minute, the second and successive rays are long and flexible, supported by distally tapered rod-like radials which tend to occur in pairs within each interneural space, their proximal tips converging (Fig. 13C,D). The origin of the dorsal fin occurs between the third and fourth neural spines. There are no supraneurals (predorsals). The anal fin has 50–58 rays and lacks a stout anterior spine; the shape of the radials is similar to those which support the dorsal fin (Fig. 13D).

Caudal fin skeleton (Fig. 15A,B). The caudal fin skeleton of *Melanonus* resembles that of the Moridae in that the first and second hypurals are incompletely fused; each support a single fin ray. In morids all the hypurals are fused only proximally whereas in *Melanonus* fusion of hypurals 1 and 2 is both proximal and distal leaving a central opening (Fig. 15A). Hypurals 3–5 although fused in specimens of *M. zugmayeri* of 130mm SL are only partially fused in 66mm and 100mm SL specimens (Fig. 15B). Paulin (1983, fig. 5A) figures a caudal skeleton of *M. gracilis* in which hypurals 1 and 2 are entirely fused and the fifth is reduced. In a 45mm SL specimen of *M. gracilis*, all the hypurals are separated for their entire lengths whereas in a 49mm SL specimen they are fused distally but not proximally. There are two elongate epurals each supporting a fin ray; in a 100mm SL specimen of *M. zugmayeri* they are joined proximally (Fig. 15B). Unlike morids, *Melanonus* lacks X and Y bones a feature shared with Macruronidae, Gadidae and Lotidae. A long parhypural articulates basally with the fused hypurals 1 and 2 and supports a single fin ray.

Comments on features of the vertebral column and median fins. Chopstick-shaped ribs, similar to those of *Melanonus*, have been reported for *Macruronus*, *Lyconus*, *Steindachneria* and *Merluccius* by Okamura (1989) and Inada (1989) who arrive at opposite conclusions with regard to their character polarity. According to Okamura this rib-type suggests a close relationship between the taxa in which they occur. Inada, on the other hand, regards them as a plesiomorphic gadoid feature. Although Inada's (1989) reasoning appear to be

based on an *a priori* assumption of merlucciid plesiomorphy I would agree with his assumption. In fact, this type of rib is more widely distributed amongst gadoids than has been reported and also occurs amongst 'supragadoids' other than Merlucciidae (Fig. 14A).

In *Melanonus* the ribs occur on vertebrae 3–5 as in *Lyconus*, but they are on vertebrae 3 and 4 in *Macruronus* (both Macruronidae), 3–6 in Merlucciidae, and 3–4 in Gaidropsaridae. In Steindachneriidae the ribs are on vertebrae 3 and 4 but the rib on the fourth has less than half the thickness of that on the third whereas in the above cited taxa the ribs are of equal thickness. Furthermore, the epipleurals attach directly to the distal tips of the chopstick ribs in *Steindachneria* whereas in the other taxa they are indirectly attached by ligamentous strands running to the myosepta (as in *Melanonus*). In morids and 'supragadoids' epipleurals are attached directly to the vertebral ribs. Patterson & Rosen (1989) interpreted the vertebral ribs *Steindachneria* and *Gadus* as a parapophysis with attached epipleural. The ribs in Steindachneriidae, however, are like those of Melanonidae, Macruronidae and Merlucciidae in articulating with the ventral cavity of the centrum. In the Bregmacerotidae the third and subsequent vertebrae bear parapophyses to which are attached cartilage-formed ribs (Fig. 14B). The loss of epipleurals from the first and second centra is a gadiform synapomorphy (Markle, 1989).

Howes (1991b) regarded the first neural arch of *Macrur-*

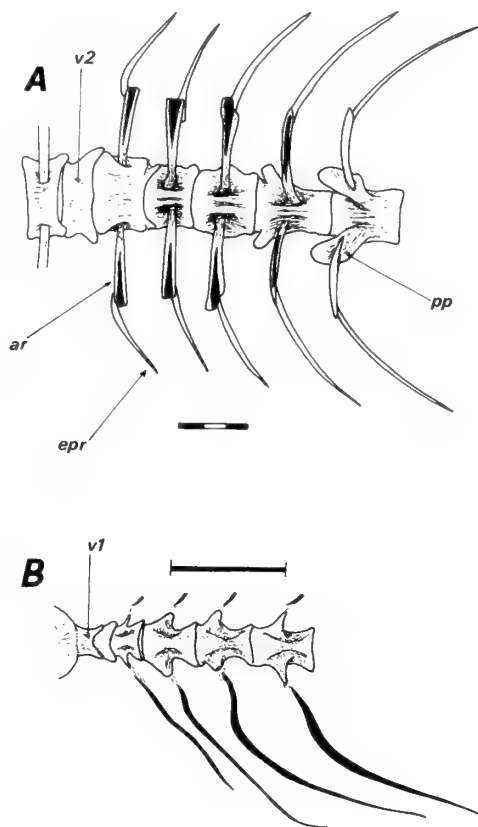


Fig. 14. Anterior region of vertebral column in: A, *Gaidropsarus mediterraneus*; B, *Bregmaceros* sp. In A, black shading in the ribs (ar) indicates zones of cartilage.

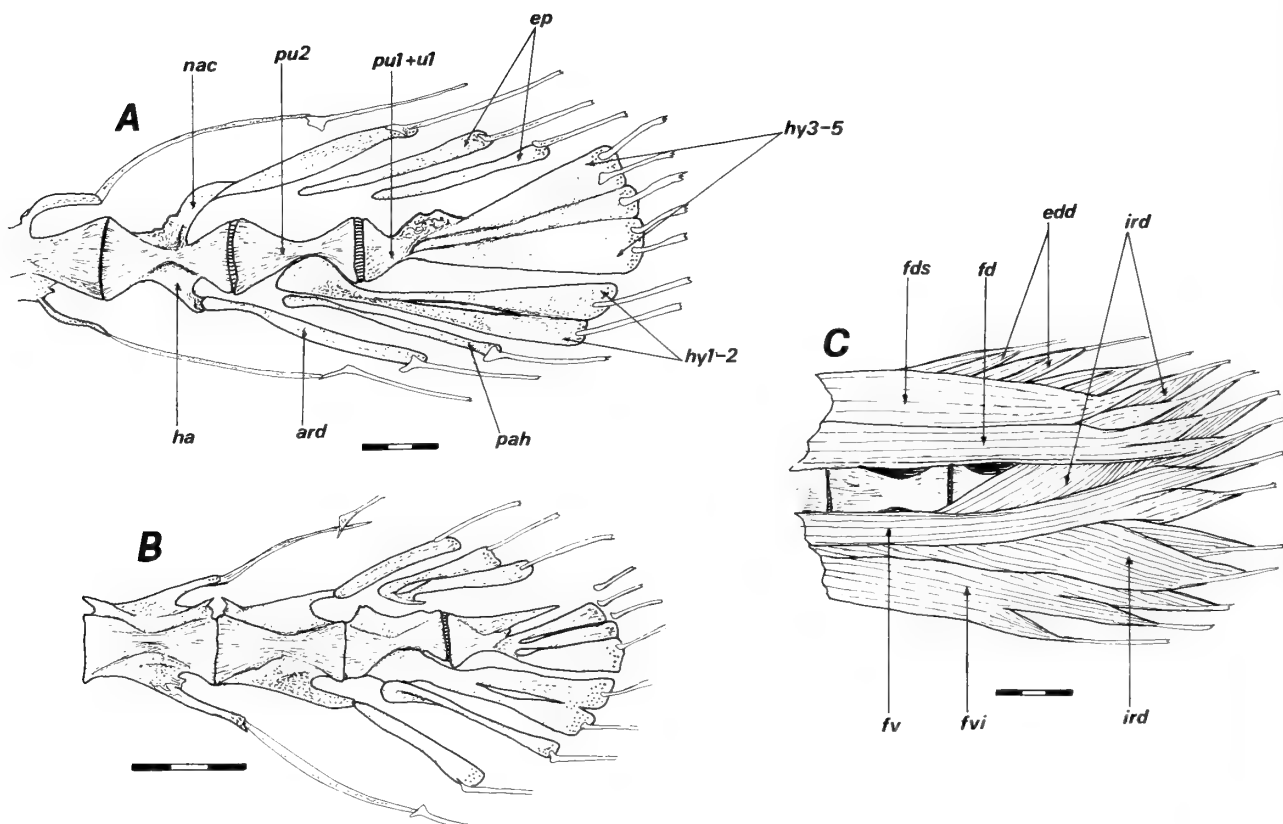


Fig. 15. *Melanonus zugmayeri* Caudal fin skeletons of A, 130mm SL and B, 100mm SL specimens. C, caudal fin musculature (although a superficial layer of connective tissue and some muscle has been removed the vertebrae are exposed *in situ* as shown).

nus (Macruronidae) as a composite unit incorporating an accessory neural arch suggesting that the first centrum had been incorporated in the 'basioccipital'. Since, however, 1) ribs are always lacking from the first two vertebrae in gadiforms, 2) Baudelot's ligament always occurs on the first centrum and 3) an accessory neural arch does not occur above aulopiforms, it seems untenable that incorporation has occurred in macruronids.

The caudal fin skeleton is lacking in the majority of gadiform taxa but where it does occur its most significant features are fusion of the upper hypurals and the presence of X and Y bones (lost in some taxa, see above), both of which contribute to the symmetry characteristic of 'supragadoids'. The morid caudal fin skeleton is regarded as the plesiomorphic gadoid type since it approaches that of most other teleosts in its asymmetry and in having distally separated hypurals. In this latter respect, *Melanonus* demonstrates a further derived condition in having the hypurals distally fused (see further discussion on p.30).

Of particular note is the condition of the *caudal fin musculature* (Fig. 15C) which differs from that described in gadoids (Howes, 1991) where *hypochordal longidorsales*, *flexores dorsales* and *inferiores* are absent, the *interradiales* have a characteristic linkage pattern between the caudal fin rays and are continuous with the dorsal and anal fin rays. Howes (1991: 104) pointed out the absence of the latter in Melanonidae, but overlooked the fact that the caudal fin musculature more closely resembles that of other paracanthopterygians and acanthopterygians in having discrete dorsal

and ventral *flexores* and an amalgamated segment of *interradialis* musculature corresponding to the superficial *interradialis*.

Melanonus, *Lyconus* and *Brosme* are the only gadiform taxa to possess a single dorsal fin, most have two and the more derived Gadidae have three. Dorsal fin origin is usually above the second and third neural spines, as in *Melanonus*, but the origin of the second dorsal is variable, the radial supporting the first ray of that fin being between the eighth and ninth, ninth and tenth or tenth and eleventh neural spines. According to Inada (1989) the single dorsal fin of *Lyconus* evolved from amalgamation of two separate fins. Inada's evidence relies on a notch being present in the fin at a point above the proximally curved thirteenth radial which lies between the eighth and ninth neural spines which as just noted is the region commonly associated with the origin of the second dorsal fin. No similar 'evidence' occurs in *Melanonus*.

Among gadoids the first radial of the first dorsal fin usually lies between the second and third neural spines, but this is variable being between the first and second in gaidropsarids, and in Bregmacerotidae the first radial has become directed forward so that the first dorsal fin ray lies above the supraoccipital. In macruronids, the first supporting radial is also usually between the second and third neural spines but sometimes between the third and fourth. Percopsids, like melanonids have the first radial between the third and fourth neural spines. In ophidiiforms the position of the first radial is variable and can lie between any of the neural spines from the

first to the tenth. In batrachoidiiforms it is usually between the third and fourth neural spines and in lophiiforms the eighth and ninth or more posterior neural spines.

Supraneurals, preceding the first dorsal fin are rarely present in gadiforms (Patterson & Rosen, 1989).

Baudelot's ligament (Figs 13A,B) stems from the lateral cavity of the first vertebra to connect with the supracleithrum. The *retractor dorsalis* muscle originates from the fourth through sixth vertebrae; on the sixth it is attached to the leading edge of the parapophysis (Fig. 13B).

Brain (Fig. 16).

The brain of *Melanonus* is situated well forward, the telencephalon and anterior part of the mesencephalon being anteriorly displaced beyond the cranial cavity so as to lie in the orbital cavity formed by the enlarged pterosphenoids. The olfactory and optic lobes are large. The olfactory tracts are well separated and each tract is short and thick comprising at least twelve separate nerves each of which branches to

feed the individual laminae of the nasal rosette. The olfactory bulb is large and lies against the lobe which is narrowly separated by a fissure from the laterally situated optic lobe. Upon leaving their respective lobes ventrally, the optic tracts cross and travel directly laterad a short distance to the eyeball which is only narrowly separated from the telencephalon. The cerebellar corpus is flat and lies pointing anteriorly between the optic lobes. This is a unique condition among gadiforms (noted by Marshall & Cohen, 1973 as diagnostic of the Melanonidae), normally the corpus is bulbous and elevated (Okamura, 1970) or lies posteriorly along the cerebellar crest. The cerebellar crest is flat and elongate flanked ventrolaterally by extensive trigeminal lobes. The cerebellar body extends posteriorly to entirely overlap the vagal lobes along the basal part of the medulla oblongata, also a unique gadiform condition. The granular eminence is large but not laterally extended. Ventrally, the inferior lobes, pineal body, hypophysis and vascular sac are all well-developed.

The brains of some gadoids and macrouroids have been described by Svetovidov (1953), Okamura (1970) and Howes

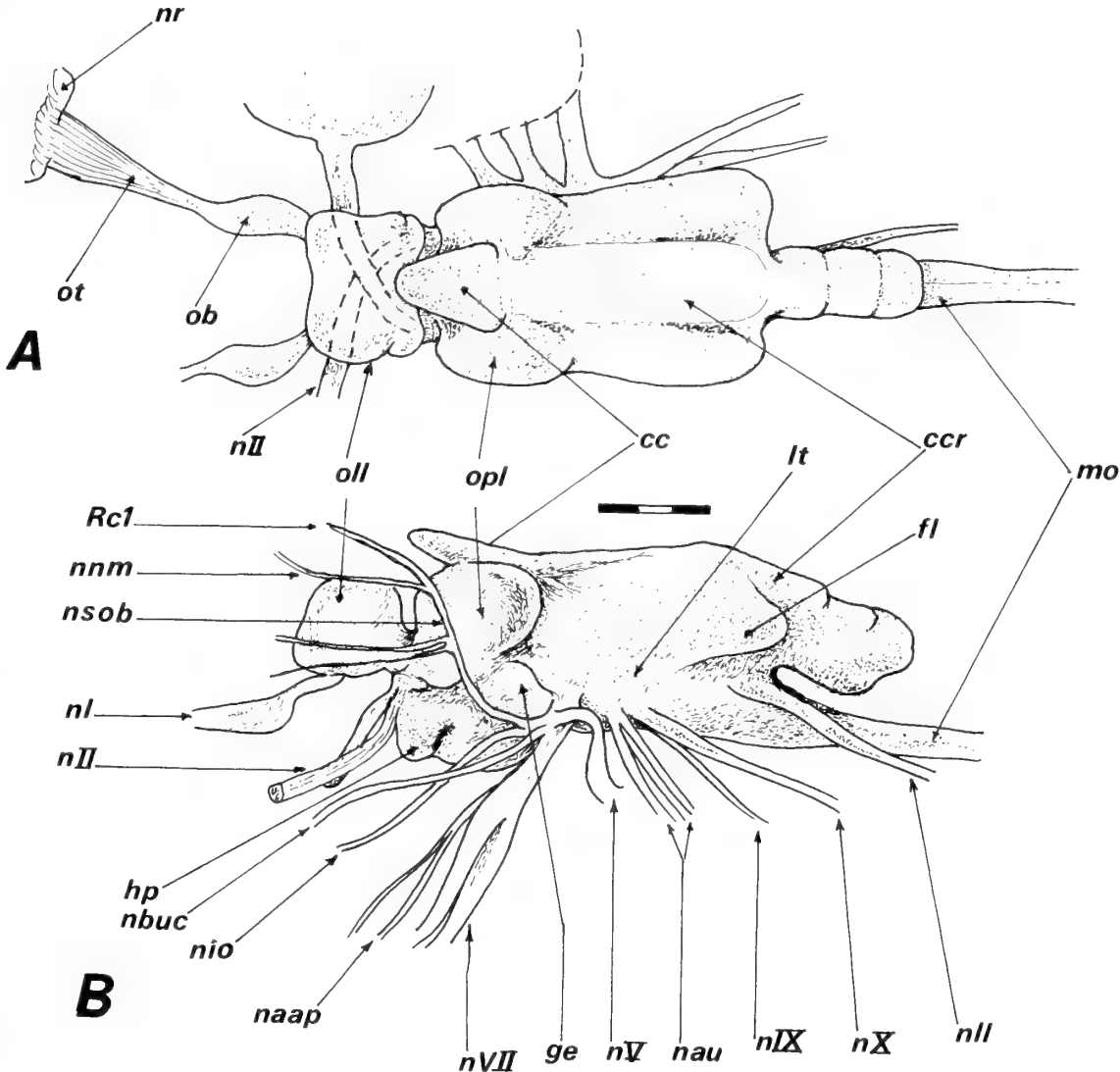


Fig. 16. *Melanonus zugmayeri* brain in A, dorsal and B, lateral views. In A, the pathways of the optic tracts beneath the lobes are indicated by dashed lines and the margin of the prootic is indicated by dashed lines lateral to the trigeminal-facial nerve complex.

& Crimmen (1990) and of those published descriptions *Bregmaceros* has the most similar overall morphology. Like that of *Melanonus* the brain is elongate with extensive trigeminal-facial lobes, a long cerebellar crest and closely connected olfactory bulb and lobe. However, there are major differences in the relatively small size of the olfactory and inferior lobes and in the cerebellar corpus being orientated posteriorly along the crest, having a posterolateral fissure and leaving the midline of the optic lobes exposed.

Anterior placement of the forebrain was considered a gadiform character by Svetovidov (1948) and among gadoids there is a tendency for the brain to be shifted forward. In those few morids investigated and in macrourids the forebrain is generally confined to the cranial cavity. In some other paracanthopterygians (ophidiiforms, Howes, 1992 and percipids pers. obs.) the telencephalon lies in the orbital cavity as in *Melanonus*.

It is problematic as to which features of gross brain morphology can be used as phylogenetic markers. The degree of separation of the olfactory bulb from the lobe is variable in gadiforms (discussed by Howes & Crimmen, 1990) but the plesiomorph condition, possessed by *Melanonus*, is seemingly for them to be closely associated. The shape of the olfactory lobe is also a highly variable feature and one that might, at least, be generically characteristic.

Summarising data from gadoid brain descriptions given by Svetovidov (1953) it appears that elongate and short cerebral crests are equally distributed amongst the taxa he studied. A short, tall cerebral crest, common to gadoid brains, is also the common condition among paracanthopterygians. However, the granular eminence, although often large is laterally extended only in the Gadidae (*sensu* Dunn, 1989 and Howes, 1991b).

Swimbladder, viscera and body musculature (Fig. 17).

The *swimbladder* is an elongate ellipsoidal, thin-walled sac adhering tightly to the vertebral column apart from where the long bilobed *kidney* runs on either side of the midline. According to Marshall & Cohen (1973) the melanonid swimbladder is reduced and there are two retia. In the specimens of *M. zugmayeri* examined for this feature, the gas-gland covers nearly two-thirds of the anterior floor of the sac and there are four retia supplying separate lobes. Posteriorly the gas-gland tapers and is deeply pocketed. The oval appears to be beneath the retial area.

The *stomach* is siphon-shaped, exceptionally thick-walled with a deeply and much convoluted mucosal membrane; there are six or seven caeca lying ventrally; the *intestine* is long and double-banded. The bilobed *kidney* is extensive, almost enveloping the stomach. The *gonads* lie posteriorly on either side of the swimbladder to which they are attached by thin strands.

The *anterior body musculature* is similar to that described for Bathygadidae (Howes & Crimmen, 1990) except that melanonids lack the same degree of differentiation between dorsal and ventral sections of the *epaxialis* musculature (Fig. 17), the dorsal section being apparent only anteriorly (the general condition) and not extended as far posteriorly as in bathygadids.

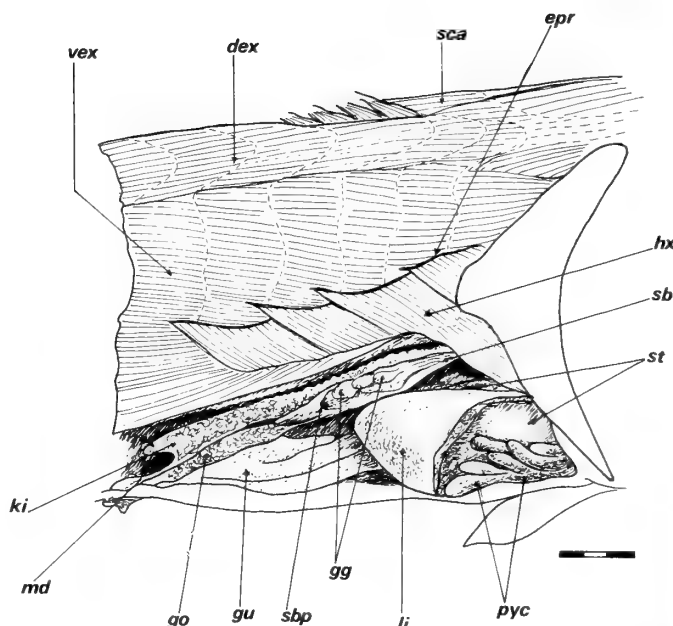


Fig. 17. *Melanonus zugmayeri* anterior body musculature and visceral cavity dissected on the right side; the anterior part of the liver has been cut away to expose the pyloric caeca and the swimbladder has been dissected.

DISCUSSION

Melanonus has undoubtedly derived sensory features; the brain has a unique morphology amongst paracanthopterygians, extending well forward into the orbital cavity, the head is covered with a unique type and pattern of open-ended neuromasts innervated by the ramus canalis lateralis of the trigeminal nerve, the RLA nerve being absent. In its cranial osteological characters three can be considered derived: the shape of the fifth infraorbital, and exclusion of the supraoccipital from contributing to the foramen magnum. The first two of these osteological characters are autapomorphic; the enlarged pterosphonoid is undoubtedly correlated with the anterior position of the telencephalon. The third is a feature shared with ophidiiforms, in that group, however, the exoccipital is expanded dorsoposteriorly so as to exclude most of or the entire supraoccipital from the rear of the cranium and from contact with the first neural spine. In melanonids the supraoccipital is excluded from the border of the foramen magnum by its failure to extend ventrad during development, but nevertheless it still forms the upper posterior border of the cranium and contacts the first neural spine.

Aside from these autapomorphies there are no other apomorphies which are shared with other gadoid taxa. The diagnosis of 'Gadoidei' has proved difficult since most synapomorphies so far proposed are either not exclusive to, or their distribution has not been completely documented, in the taxa currently embraced under this category (see below).

Howes (1990; 1991a; 1991b) proposed a series of gadoid clades of which 'supragadoids' were recognised on the basis of a fused upper hypural plate of the caudal skeleton. A sequence of other synapomorphies, including an interopercular fossa, contact of the posterior face of the lateral ethmoid wing by the first infraorbital and reduction of pterygoid bones (Howes, 1990) excluded Melanonidae from this group. Other

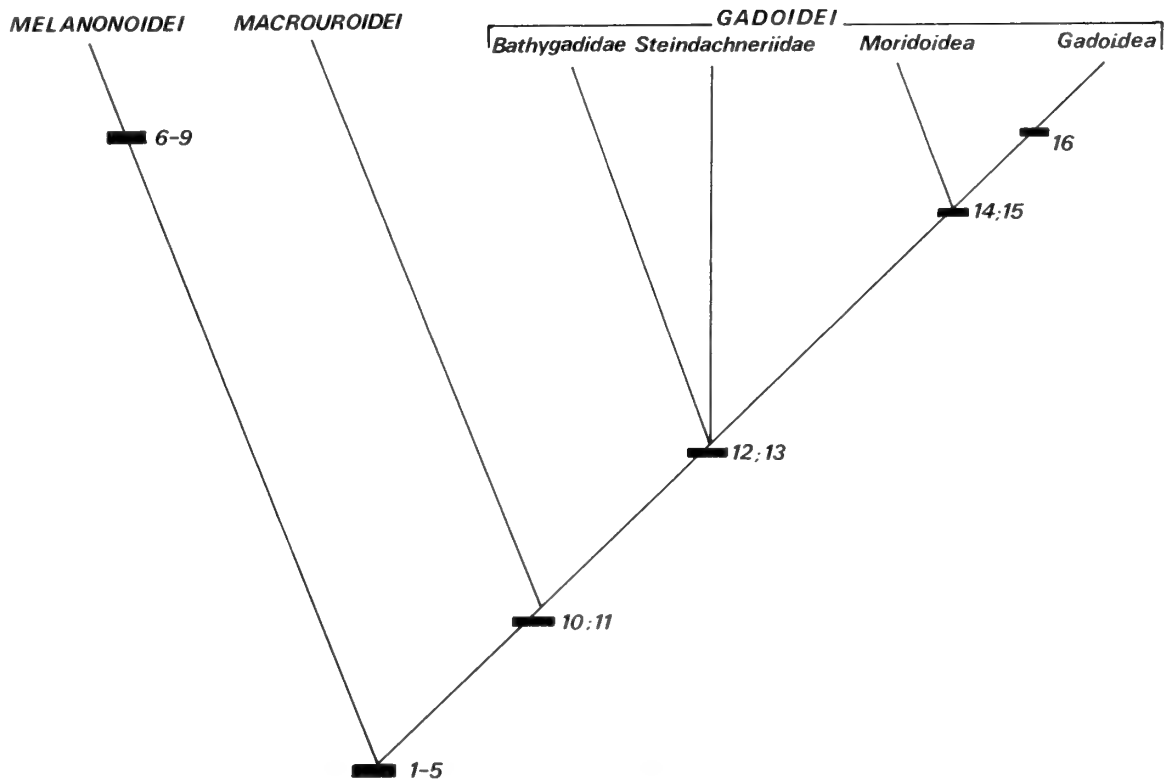


Fig. 18. Proposed relationships of Melanonoidei with other gadiforms. *Synapomorphies*: 1, absence of pars jugularis, i.e. common aperture for principal cranial nerves (also occurs in some ophidiiforms); 2, loss of intermusculars from vertebrae 1 and 2; 3, scapular-coracoid foramen; 4, attrition of lateral face of hyomandibular; 5, levator arcus palatini covers lateral face of jaw musculature; 10, palatine forming a hinge or butt-joint with pterygoids; 11, enlarged intercalar contributing to posterior wall of cranium; 12, pharyngohyoideus muscle mediated by sternohyoideus; 13, interradales muscle connected to dorsal and anal fin rays, loss of various caudal fin muscles and entire caudal skeleton in some taxa; 14, palatine contacts mesethmoid; 15, X and Y bones in caudal skeleton (lost in some taxa); 16, complete fusion of upper hypurals and symmetry of hypural plates. *Autapomorphies* for Melanonoidei: 6, supraoccipital excluded from margin of foramen magnum; 7, cranial neuromast pattern and innervation; 8, brain position and morphology; 9, enlarged pterosphenoids contacting lateral ethmoids. *Synapomorphies* 1–5 and 10–11 from Gosline (1968; 1971); Howes (1988; 1989; 1990; 1991b); Markle (1989); Patterson & Rosen (1989). *Synapomorphies* for macroroids summarized by Iwamoto (1989) and Howes & Crimmen (1990) and for moridooids by Paulin (1983).

taxa so excluded are Moridae, Eulichthyidae, Steindachneriidae and Bathygadidae. The two latter lack a caudal fin skeleton, thus the incomplete fusion patterns of hypural bones possessed by morids, eulichthyids and melanonids cannot be extended to these taxa. The cranial and vertebral osteology of Bathygadidae is plesiomorphic in comparison to other gadoid taxa whereas that of Steindachneriidae is relatively derived (pers. obs. see also Fahay's, 1989, notes on pelvic girdle morphology).

The Melanonidae lacks a feature common to other gadiforms (macroroids + gadoids), namely, a short palatine forming a butt or hinge joint with the ento- and ectopterygoids. In almost all gadiforms the palatine has a truncated near vertical margin which forms a mobile (laterally expanding) joint with the anterior margins of the pterygoid bones (p.20). *Melanonus* has a plesiomorphic palatine where the stem firmly contacts the margin of the ectopterygoid. Moreover, the palatine extends some distance along the ectopterygoid and is toothed. Since no other gadiform has palatine teeth it might be assumed that the melanonid palatine is the primitively composite dermo- and autopalatine whereas other gadiforms have lost the dermal component. In other paracanthopterygians, ophidiiforms and lophiiforms possess the plesiomorphic, long posteriorly extended and toothed palatine;

percipids resemble gadiforms more closely in having an edentulous bone which abuts the straight anterior margins of the ecto- and entopterygoids but which still retains a posteriorly directed stem (p.20).

The Melanonidae possesses three of those characters identified by Patterson & Rosen (1989) and Markle (1989) as gadiform synapomorphies or potential synapomorphies, namely, absence of epipleural ribs from the first and second vertebrae; a scapular-coracoid foramen and absence of a lateral commissure, cranial nerves I–VII exiting through a common aperture. Two other potential synapomorphies listed by Patterson & Rosen (1989) are presence of X and Y bones and liver LDH pattern. X and Y bones are absent in melanonids and can only be judged as a plesiomorphic state or, against the congruence of other synapomorphies, as secondary loss. In the latter case the feature then appears as synapomorphic for a subgroup of gadoids (Fig. 18). LDH liver pattern has not been tested for in this taxon.

Two other synapomorphies appear to be: 1) the form of the hyomandibular, which in the majority of gadoids and macroroids has attrition of the anterior border and lateral face, fully or partly exposing the pathway of the hyoid branch of the facial nerve (Howes, 1989; 1991b; 1992); 2) the levator arcus palatini covering the adductor mandibulae musculature

laterally (Howes, 1988; 1991b).

Melanonids have a small intercalar, a bone which in other gadiforms contributes to a substantial part of the lateroposterior cranial wall. In size the melanonid intercalar approaches that of *Percopsis*. Whether in *Melanonus* the bone is plesiomorphically small or whether there has been reduction secondarily can only be assessed against the distribution of other, known derived features (Fig. 18). An intercalar is absent in lophiiforms and batrachoidiforms, an assumed secondary loss (Patterson & Rosen, 1989).

The single dorsal fin is probably a plesiomorphic feature (p. 26). Among paracanthopterygians, an elongate second dorsal fin is assumed to be synapomorphic for anacanthines (*sensu* Patterson & Rosen, 1989). Melanonids share with ophiidiiforms (including carapids and bythitoids), two gadoid genera (*Lyconus* and *Brosme*) and Macrouroididae a single dorsal fin which must be seen as resulting from either the 'loss' of the first dorsal with anterior encroachment of the second, or the amalgamation of the two fins. It is impossible to distinguish between such phylogenetic events although either way the condition is seen as derived. Iwamoto (1989) considered the single dorsal fin of macrouroidids to be derived but that of the gadoid *Brosme* as plesiomorphic retention. Judging by the incongruent distribution of the character it is almost certainly homoplastic. The further partitioning into three fins in Gadidae represents a further derived state.

In jaw musculature melanonids are little different from morids and bathygadids (Howes, 1988). Howes (1990; 1991b) noted a medial shift of adductor muscle A1b which would suggest a close phylogenetic relationship with supragadoids. This shift, however, is apparently induced by the presence of a unique transverse ligament which runs from the palatine to the inner face of the second infraorbital and which constricts and turns A1b inwards. This is not the same condition as the entire medial shift of an unconstricted A1b in 'supragadoids'.

Melanonids have an unusual condition of the hyoid musculature whereby the *pharyngohyoideus* (= *rectus communis*) attaches to the third hypobranchial as well as the urohyal (Howes, 1988). Urohyal attachment of the *pharyngohyoideus* is shared with macrouroids, two gadoid families and all other ctenosquamates (Lauder, 1983; Howes, 1988); in remaining gadoids the *pharyngohyoideus* is mediated by the *sternohyoideus*. It is assumed that the two exceptional gadoid families (Muraenolepididae and Ranicipitidae) have lost the *sternohyoideus* attachment, the *pharyngohyoideus* being attached to the tip rather than the lateral face of the urohyal keel as it is plesiomorphically in melanonids.

The melanonid caudal fin musculature (p. 26) lacks those features regarded as synapomorphic for gadoids (since macrouroids lack caudal fin skeletons and associated musculature it cannot be known whether this derived form of muscle arrangement was a gadiiform feature subsequently lost in macrouroids). Melanonids have a caudal fin muscle arrangement only slightly modified from that present in other paracanthopterygians and in acanthopterygians.

Although it cannot be doubted that the Melanonidae belongs among Gadiformes there is no evidence to suggest that it be regarded as a member of the Gadoidei. To be included within the Gadoidei, the elongate toothed palatine, lack of X and Y bones, reduced intercalar and single dorsal fin must be regarded as reversal and loss characters. The caudal fin skeleton demonstrates an advanced condition to that of the Moridae (the plesiomorphic gadoid taxon) in

having, in adults, almost complete fusion of the upper hypurals which alone, would signify inclusion within the 'supragadoids'. Indeed, I have argued elsewhere (Howes, 1991b: caption to fig. 35) that the reported separation of hypurals in young ranicipitids (which I place amongst the 'supragadoids') is a character reversal; a conclusion drawn on what appears to substantial support from other synapomorphies. In the case of melanonids the principal evidence against the caudal fin skeleton being a character reversal is that the associated musculature has a plesiomorphic arrangement, lacking those derived elements found in the musculature of morids and other gadoids, including ranicipitids (as an adult, *Raniceps* has the typically symmetrical gadoid caudal fin skeleton, lacking in *Melanonus*). Thus the fusion or partial fusion of the upper hypurals in melanonids is considered to have occurred independently to that in gadoids above the morid level.

Taking into account these arguments and the anatomical evidence presented herein, the Melanonidae is regarded a basal gadiform taxon, representing, as Markle (1989) had previously hypothesised, the sister-group to both gadoids and macrouroids (Fig. 18). Such a phylogenetic arrangement leads to a higher level re-classification of the Melanonidae. Following Markle (1989) and recognising the family as being phylogenetically coordinate with the Macrouroidei and Gadoidei, it is placed in the suborder Melanonoidei. Those taxa which I have previously recognised as a monophyletic group termed 'supragadoids' are equivalent to Markle's (1989) Superfamily Gadoidea. The Moridae and Eulichthyidae are regarded by Markle (1989) as sister taxa on the basis of asymmetry of procurrent caudal fin rays; I know of no supporting osteological synapomorphies for this relationship but provisionally accept it. Together these taxa form the sister-group to the Gadoidea and as such must be regarded as the Superfamily Moridoidea (= Moriformes, part, Schwarzhans, 1984). The 'infragadoids', Steindachneriidae and Bathygadidae have no such status since they form an unresolved polychotomy with the Gadoidei + Moroidei and Macrouroidei.

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A review of the serranochromine cichlid fish genera *Pharyngochromis*, *Sargochromis*, *Serranochromis* and *Chetia* (Teleostei: Labroidei)

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SYNOPSIS. Recent taxonomic changes, newly described taxa and groups of taxa, and the introduction of taxonomic characters not previously employed require a revision of the informally recognised, essentially fluviatile group of southern African cichlids, the so-called serranochromines. The genera included in this assemblage are *Pharyngochromis*, Greenwood, *Sargochromis* Regan, *Serranochromis* Regan, and *Chetia* Trewavas.

Previously, *Sargochromis* was considered to be a subgenus of *Serranochromis*, but new evidence indicates that it should be reinstated as a distinct lineage (*i.e.* genus). The species originally described as *Serranochromis* (*Sargochromis*) *gracilis* should now be transferred to the genus *Chetia*. Formerly the latter taxon was thought to be monotypic, but it is now expanded to include five species. One of these, *Chetia brevis* Jubb, had been included tentatively in the genus *Astatotilapia*, but is now returned to the genus in which it was described originally.

The monophyletic origin of the serranochromines has still to be established. For that, and other reasons, doubt is cast on the phylogenetic reality of the '*Pharyngochromis* – *Chetia* – *Serranochromis*' group of endemic species in Lake Malawi. The suggested interrelationships of the serranochromine genera presented below, and based on shared derived characters, cannot, for the same reasons, be considered a truly phylogenetic one.

INTRODUCTION

In a paper (Greenwood, 1979) reviewing and reconsidering the generic classification of several cichlid taxa then referred to the genus *Haplochromis*, an informal group of three genera was recognised on the basis of its constituent species having particular types of squamation and anal fin markings (*op. cit.*: 229–316). The group was, and still is considered one of convenience because no cladistically based hypothesis could be erected to establish the monophyly of its contained genera, *viz.* *Serranochromis* Regan, 1920 (with which was incorporated, as a subgenus, *Sargochromis* Regan, 1920), *Chetia* Trewavas, 1961, and *Pharyngochromis* Greenwood, 1979. A scheme of possible interrelationships of these taxa,

suggested earlier by Trewavas (1964), was also discussed in my 1979 paper.

Recent studies of the genera call for a revision of the group's taxonomy at the generic level, and a reconsideration of their possible interrelationship. For example, the genus *Chetia*, treated as monotypic by Greenwood, (1979) is now thought to contain five species (Balon & Stewart, 1983; Greenwood, 1984, 1992, and below, p. 38), certain problems regarding the generic classification of several Angolan haplochromine species have been clarified (Greenwood, 1979, 1984 & 1992), new ideas on the supposed relationship of *Serranochromis* and *Sargochromis* have been put forward by Lippitsch (1991: 99–100), and Eccles & Trewavas (1989: 21) have formally recognised, amongst the endemic genera of Lake Malawi, a large assemblage of species which they

designate 'The *Pharyngochromis* – *Chetia* – *Serranochromis* group'.

The term 'serranochromine' will be used in this paper as a group name for the genera *Chetia*, *Serranochromis*, *Sargochromis* and *Pharyngochromis*. Its use should not be construed as an indication or even a presumption of the group's ultimate and formal recognition as a Tribe. In the sense employed here it is comparable with my earlier use of the informal categories 'haplochromines' and 'pelmatochromines' (Greenwood, 1979 & 1987). Such continued use, and introduction, of informal groupings clashes with the tribal status given by Poll (1986) to several cichlid assemblages in Lake Tanganyika, and with the geographically and taxonomically more extensive tribe Haplochromini defined by Eccles & Trewavas (1989), a tribe which also includes the serranochromines. In my view, these authors' actions are premature. Too few critical higher-level taxonomic studies have yet been made on the Cichlidae to support the phylogenetic relationships that are (or should be) implicit in the award of formal tribal status. For instance, Eccles & Trewavas (1989: 21) define the Haplochromini as: "Maternal mouth-brooding cichlid fishes of Africa and the Jordan Valley in which the basioccipital bone participates with the parasphenoid to form the apophysis for the upper pharyngeal bones". The value of the apophyseal character has been questioned by several authors (see review in Greenwood, 1978, also Greenwood 1986) and it may have evolved more than once among African taxa (Greenwood, 1987); maternal mouthbrooding has apparently evolved independently in both the Tilapiini and Haplochromini (the tribes, respectively, *sensu* Trewavas, 1983, and Eccles & Trewavas, 1989), and in one species of the genus *Chromidotilapia* of the pelmatochromines (*sensu* Greenwood, 1987: 169) in which paper it is also argued (*op cit*: 194–199) that this group should not be included, as it was by Trewavas (1983), in the tribe Tilapiini.

Thus, the purpose of the present paper is simply to clarify the taxonomic status of the 'serranochromine' genera, and to establish a basis for further and phylogenetic studies of those taxa and those of Lake Malawi.

METHODS AND MATERIALS

ANAL FIN SPOTS AND TRUE OCELLI. One of the features used to define the serranochromines is the presence of maculae on the anal fin, usually in both sexes (Greenwood, 1979). A distinction was made there between true ocelli (such as occur, but almost exclusively in males, in a large number of haplochromine species, e.g. those in Lakes Victoria, Edward and Kivu), and the spots or maculae found in the serranochromines and the haplochromines of Lake Malawi (see figure in Eccles & Trewavas, 1991). Judging by a recent description of a new *Serranochromis* species (Winemiller & Kelso-Winemiller, 1991) it is clear that some confusion still exists when discriminating between these two kinds of anal fin markings. Granted, it is often difficult to do so when only preserved material is available, but in life the difference is obvious, as colour photographs in aquarium books will show (e.g. Konings, 1991).

The densely pigmented ovoid or near circular centre of the true ocellus, usually circumscribed by a narrow, darkly pigmented ring, is surrounded, or almost surrounded, by a zone of virtually transparent, or at least freely translucent, and

apparently unpigmented fin membrane. This clear zone is of variable width and outline, but is often concentric with that of the pigmented centre. In life, the clear zone seems to emphasise the coloured central area, thereby making it stand out from the rest of the fin membrane, be that membrane pigmented or hyaline. In colour photographs of live or freshly dead specimens, the clear zone often appears to be dark or even black, a result either of the dark background against which the fish was posed, or the shadow cast by the fish's body and the anal fin itself. To the best of my knowledge, true ocelli do not occur, at least in nature, on any of the other paired fins, although these fins are often maculate. Anal ocelli are also of rare occurrence in females, but large non-ocellate spots are sometimes present on that fin in the females of species whose males have true ocelli. The spots in such females occupy the same position as the ocelli in males, and are often of the same size. As compared with maculae (*i.e.* non-ocellate spots) on the anal fin, true ocelli are generally larger, and are always readily distinguishable from the maculae on the other unpaired fins.

In contrast, non-ocellate anal spots, besides usually being smaller than ocelli, are, with few exceptions (see Greenwood, 1992) more numerous and differ little in their overall appearance from those on the other fins, although the central pigmented portion may differ quite markedly in colour. The essential difference between maculae and ocelli, however, lies in the absence of a transparent or freely translucent area surrounding the pigmented centre of a macula, which, like that of an ocellus, is bounded by a very thin ring of dark pigment. Instead, the macula's pigmented centre is circumscribed by a ring, usually narrow, of lighter pigment which separates it from whatever ground colour the fin membrane may have.

This outer, lightly pigmented ring is not visible in some of the preserved serranochromine specimens I have examined, and the central spot is bounded only by the very narrow ring of dark pigment separating it from the chromatophores in the fin membrane. Whether or not this situation is a preservation artefact cannot be determined at present.

In their account of the anal fin markings in the newly described species *Serranochromis altus*, Winemiller & Kelso-Winemiller (1991: 679) describe, unfortunately without an illustration, the fin in both sexes as having "... 30–40 large pink or pink-orange ovate spots, each ringed with a transparent, white ocellus. . .". I would suggest that the use of the words 'transparent and white' in apposition is somewhat contradictory, and that 'translucent white' would describe the condition more accurately, especially since it is one I have seen in fresh specimens of *Serranochromis* (and *Sargochromis*) species from the Okavango river and swamp system in Botswana.

PRESHANK LENGTH OF THE MAXILLA; LENGTH OF THE PRE-MAXILLARY ASCENDING AND ALVEOLAR PROCESSES. The preshank length of the maxilla, relative to its shank length, and the length of the alveolar process of the premaxilla relative to the length of the entire ascending premaxillary process, are two morphometric characters not used in earlier papers (Greenwood, 1979, 1989, 1981).

Preshank length of the maxilla is measured, on the bone's medial aspect, from the anterior tip of the medial arm of the maxilla's saddle process, to the mid-point of the anterior vertical projection from the upper margin of the bone's shank (see Fig. 1). Shank length is measured, also directly and on

the bone's medial aspect, from the midpoint of the vertical projection to the posterior point on the maxilla's posterior margin (see Fig. 1).

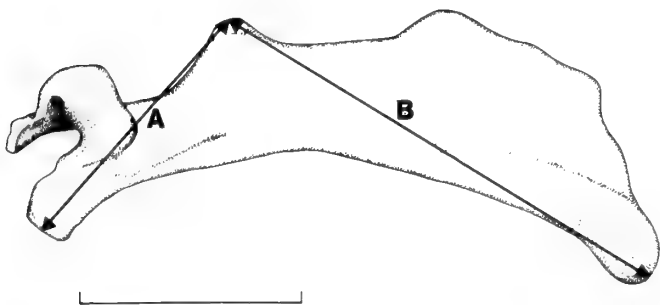


Fig. 1. Medial aspect of maxilla (from *Serranochromis macrocephalus*), viewed somewhat dorsolaterally, to show points of measurement for: A, preshank length, and B, shank length. Scale bar = 5 mm.

The length of the premaxilla's ascending process is measured, directly, from the dentigerous surface of the bone at its symphysis with the premaxilla of the opposite side, to the dorsal tip of the process. The length of the alveolar process uses the same ventral (*i.e.* dentigerous surface) reference point; its dorsal limit being the highest point on the dorsal margin of the process (see Fig. 2).

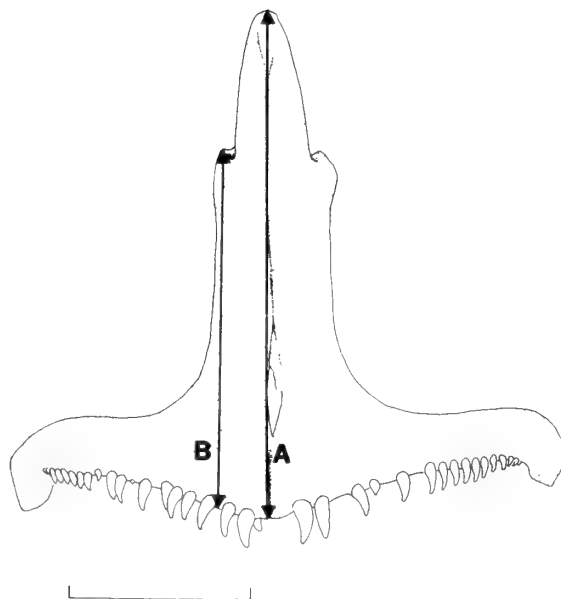


Fig. 2. Frontal view of left and right premaxillae (from *Serranochromis macrocephalus*) to show points of measurement for: A, height of ascending process, B, height of alveolar process. Scale bar = 5 mm.

STUDY MATERIAL

See Greenwood (1979, 1984, 1992) for specimens used in previous studies of *Serranochromis*, *Sargochromis*, *Chetia* and *Pharyngochromis*. Additional material:

- Sargochromis coulteri* RUSI 26627. Namibia (4 specimens)
- Sargochromis coulteri* RUSI 36419. Namibia (1 specimen)
- Sargochromis coulteri* RUSI 28106. Namibia (1 specimen)
- Sargochromis giardi* RUSI 35782. Zambia (3 specimens)
- Sargochromis carlottae* RUSI 31204 Namibia (3 specimens)
- Sargochromis carlottae* RUSI 31214 Namibia (2 specimens)
- Sargochromis coulteri* RUSI 31199. Namibia (1 specimen)
- Serranochromis robustus* RUSI 31169. Botswana; Okavango river (1 specimen)
- Serranochromis thumbergi* RUSI 22660. Dam, Empangeni area, Natal R.S.A. (1 specimen presumably an introduction)
- Serranochromis longimanus* RUSI 23877. Botswana; Okavango swamps (6 specimens)
- Serranochromis macrocephalus* RUSI 24175. Botswana; Boro river (9 specimens)
- Serranochromis angusticeps* RUSI 26854. Okavango swamps (4 specimens)
- Chetia brevis* Holotype AMG. P. 951. Lomati river, R.S.A.
- Chetia brevis* Paratypes AMG. P. 952. Lomati river, R.S.A. (5 specimens)
- Chetia brevis* AMG. P. 1422. Lomati river, Barbeton district, R.S.A. (3 specimens, one partly skeletonized; see below)
- Chetia flaviventris* AMG. P. 1298. Mogel river, Waterberg, R.S.A. (7 specimens, one partly skeletonized; see below)
- Chetia flaviventris* AMG. P. 6871. Tweeport, Rustenburg district, Limpopo system, R.S.A. (10 specimens)

Chetia flaviventris Palala river at Muisvogelkraal (24° 00'S, 28° 24' 30"E) R.S.A. (5 specimens)

Chetia mola Holotype. ROM 29825. Luonga river (Zaire drainage), Zambia

Skeletal material

- Pharyngochromis acuticeps* RUSI 36553. Okovango river (see also Greenwood, 1992)
- Sargochromis carlottae* RUSI 31204. Namibia
- Sargochromis carlottae* RUSI unregistered. 142 mm S.L.
- Sargochromis giardi* RUSI unregistered 210 mm S.L.
- Sargochromis giardi* RUSI unregistered 244 mm S.L.
- Sargochromis cf Sargo. greenwoodi* RUSI unregistered
- Serranochromis macrocephalus* RUSI 24175. Botswana, Boro river
- Serranochromis macrocephalus* RUSI unregistered 107 mm S.L.
- Serranochromis macrocephalus* RUSI unregistered 220 mm S.L.
- Serranochromis macrocephalus* RUSI unregistered ca 220 mm S.L.
- Serranochromis angusticeps* RUSI unregistered 220 mm S.L.
- Serranochromis angusticeps* RUSI unregistered 230 mm S.L.
- Serranochromis angusticeps* RUSI unregistered 410 mm S.L.
- Serranochromis longimanus* RUSI unregistered 150 mm S.L.
- Chetia flaviventris* AMG P. 1298. Mogel river, Waterberg, R.S.A.
- Chetia brevis* AMG P. 1422. Lomati river, R.S.A.

Institutional abbreviations:

- AMG: Albany Museum, Grahamstown
- ROM: Royal Ontario Museum, Toronto
- RUSI: J.L.B. Smith Institute of Ichthyology, Grahamstown

SERRANOCHROMINE TAXONOMY

Introduction

In their revision of certain haplochromine genera from Lake Malawi, Eccles & Trewavas (1991: 21) divide the non-tilapiine taxa of that lake into three groups, one of which they call the *Pharyngochromis* – *Chetia* – *Serranochromis* group. That action I consider to be premature, both because there is little concrete information available about the phyletic inter- and intrarelationships of the Malawi species, and because, as Eccles & Trewavas point out, there are differences between the squamation of those species and that of the serranochromines as construed in this paper (see p. 40). Granted, I have suggested (Greenwood, 1979: 314) that *Serranochromis*- and *Chetia*-like taxa could have been involved in the origin of the Malawian cichlid flocks, but that idea was not put forward on the basis of characters constituting a testable hypothesis. Rather, it was intended, because of the superficial resemblance between the two groups, to promote an awareness that possible intergroup synapomorphies should be looked for in future research.

As recognised in this paper, the serranochromines are an assemblage of mainly fluviatile taxa whose geographical range encompasses the Zambezi, Save-Runde, Limpopo, Cunene, Quanza, Okavango and Zaire river systems, with one species (*Serranochromis robustus robustus* [Günther]), occurring in Lake Malawi (see Balon & Stewart, 1983; Bell-Cross, 1975; Eccles & Trewavas, 1989; Greenwood, 1984, 1992; Jubb, 1967, 1968; Ladiges, 1964; Poll, 1967; Skelton, 1993; Trewavas, 1961, 1964).

Since the last published inventory of serranochromine species (Greenwood, 1979), revisional studies (Greenwood, 1984, 1992) and the description of new species (Balon & Stewart, 1983; Winemiller & Kelso-Winemiller, 1991, and Greenwood, 1984 [see p. 38 below]) have both increased the number of included taxa and extended the geographical range of the group.

Morphologically, the two distinguishing features of the serranochromines are the following. (i) The presence, often in both sexes, of non-ocellate maculae (see p. 34) on the anal fin. Generally these spots are very numerous with, in certain species, as many as 30–40 covering almost the entire fin. However, their number and size show considerable intraspecific (and intergeneric) variability, with as few as three or four large spots occurring in some individuals of a species where the maximum number is 18–20 (Greenwood, 1992). When many spots are present their arrangement may give the impression of an irregular distribution on the fin, but (as was noted by Oliver [1984], *pace* Greenwood, 1979: 315) there is a basically linear regularity in their arrangement. (ii) All scales above the lateral-line series are cycloid, as are the majority of scales below that level. Some weakly ctenoid scales may occur anteriorly on the flanks, especially in small specimens, the ctenii being confined to a narrow arc situated near the centre of the scale's free margin.

A third but less trenchant feature of the serranochromines, as compared with other fluviatile non-tilapiine and non-pelmatochromine taxa (both *sensu* Greenwood, 1987: 194–199) is a tendency for there to be a higher modal number of abdominal vertebrae (modes 16 or 17 in serranochromines, [but 14 in one taxon] cf 12 or 13 in the other taxa); however,

the ranges for total vertebral counts in the two groups overlap.

Where information is available on breeding habits, the serranochromine species are known to be female mouth-brooders, and in all taxa the neurocranial apophysis for the upper pharyngeal bones is formed from the parasphenoid and the basioccipital bones. In those respects, the group would conform with Eccles & Trewavas' (1989) definition of the tribe Haplochromini.

Recently, Lippitsch (1991) drew attention to the possible value of scale morphology and patterns in resolving certain problems of intergeneric relationships within the serranochromines. To determine if the features described by Lippitsch could also provide another 'group' characteristic, I examined, at a magnification of 50x, the superficial morphology of flank and other scales in several species belonging to both subgenera of *Serranochromis* (*sensu* Greenwood 1979; but see p. 37), all species of *Chetia*, and in different populations of the single *Pharyngochromis* species. In general I found a fairly high level of intrageneric variability, as well as some individual variability in the features noted by Lippitsch (1991: 99–100; figs D & E) *i.e.* ornamentation of the caudal field, and the presence of a soft caudal rim to the scale. Further studies will be necessary before the value of these features can be established, both at the group and lower levels of serranochromine taxonomy. However, another squamation feature noted and discussed by Lippitsch, namely the number of scale rows between the posterior orbital margin and the preoperculum, has proved of considerable value in reviewing generic level taxonomy within this group.

The generic or subgeneric status of Serranochromis Regan, 1920, and Sargochromis Regan, 1920, reconsidered.

In an attempt to revise the *Haplochromis* generic concept on phyletic lines, several so-called *Haplochromis* species were assigned, as a subgenus, to the genus *Serranochromis* (Greenwood, 1979). Since one of these species is the type of Regan's genus *Sargochromis* (*S. codringtoni* [Blg, 1908]) that name was resurrected for the new subgenus.

The principal argument for this taxonomic rearrangement was that the taxa included in the new concept of *Serranochromis* all share what appeared to be three derived features, *viz.* an increased number of abdominal vertebrae, higher gill-raker counts, and an increased number of branched rays in the dorsal fin (Greenwood, 1979: 299).

In the light of new data, especially those stemming from an increased knowledge of the genus *Chetia* (see p. 38) and, particularly, Lippitsch's (1991) observations on the different type of postorbital squamation patterns present in the two presumed subgenera, I would now revise my earlier action and recognise both *Serranochromis* and *Sargochromis* as distinct lineages, and thus accord each generic status. The reasons for that action are as follows.

Firstly, as Lippitsch (1991) noted, in *Serranochromis* but not in *Sargochromis* there are at least two, and often more, vertical rows of scales between the posterior orbital margin and the upper part of the preoperculum's ascending arm. In *Sargochromis* only a single row is present. A double row, however, also occurs in *Chetia* (personal observations, see below). Further investigation of both *Serranochromis* and *Chetia* reveals that the double and multiple scale row condition is correlated with underlying osteological and myological

characters that are not present in *Sargochromis* or *Pharyngochromis*, the two other serranochromines with only a single postorbital scale row. These correlated features are an increase in the relative size and bulk of the upper part of the *levator arcus palatini* muscle, and an anteriorly directed lengthening of the postorbital process from the sphenotic bone, particularly its ventral region associated with the origin of the muscle (see fig. 3 and fig. 8 in Greenwood, 1992). In *Sargochromis* and *Pharyngochromis* the muscle is relatively smaller, and the postorbital sphenotic process has the almost uniformly narrow form (Fig. 3) found in the generalised haplochromine skull (and, it may be added, the skulls of *Tylochromis* and *Heterochromis*, the genera thought to represent the least derived lineages of African cichlids; see Oliver, 1984, and Stiassny, 1989 & 1991).

The other reason for reconsidering the subgeneric status of *Sargochromis* is the increased information now available, especially for *Chetia* (see p. 38), which clearly indicates an extensive overlap in the gill-raker and dorsal fin-ray characters previously used (Greenwood, 1979) to define *Serranochromis* (then including *Sargochromis*). These characters, therefore, no longer can be considered synapomorphic for *Serranochromis* and *Sargochromis* alone.

With the elimination of those two characters, the only derived feature shared uniquely by *Serranochromis* and *Sargochromis* is the increased number of abdominal vertebrae. Against that presumed synapomorphy must be set the derived postorbital scale-row character shared only by *Serranochromis* (*sensu* Regan, 1920) and *Chetia*, which genera also share two apomorphic features not previously recognised. These are: (i) an increase in the range and modal number of caudal vertebrae (range 15–18, modes 16 and 17 in *Serranochromis*, range 15–17 modes 16 and 17 in *Chetia*, compared with ranges of 12–16 in *Sargochromis*, and 14–16 in *Pharyngochromis*, with modes of 14 and 15, and 15 in the genera respectively); (ii) an increase in the range and modal number of circumpenduncular scale, *viz.* 18–20, rarely 16, in *Serranochromis* and *Chetia*, neither taxon with a clear-cut modal number, as compared with 16 or 18 (mode 16) in *Sargochromis* and 15 or 16 (mode 15) in *Pharyngochromis*. The recognition of this feature as an apomorphy is based on the circumpenduncular counts for *Tylochromis* and *Heterochromis* (see above), where the range, and modes, are 15–16.

Thus, taking into account the presumed derived characters shared only by *Serranochromis* and *Chetia*, it would seem that the higher count of abdominal vertebrae in *Serranochromis* and *Sargochromis* should be treated as a homoplasy and not, as previously thought, an apomorphy indicating an immediate common ancestor for the two taxa. For that reason I agree with, and now formally act upon Lippitsch's (1991) conclusion that "It seems advisable . . . to recognise *Sargochromis* as a distinct genus. . .".

The possible relationship of *Sargochromis* within the serranochromines is discussed on p. 41, and a revised generic diagnosis is given on p. 42.

A few further comments need to be made about the genera *Serranochromis* and *Sargochromis*. The number of postorbital scale rows in certain *Serranochromis* species can be as high as four or five, and, as far as I can determine, the number of rows is relatively constant intraspecifically. At present insufficient information is available on possible inter- or intraspecific differences in scale ornamentation, or on such variation in the presence or absence of a soft free margin to the scales (see Lippitsch, 1991). The small sample of species I

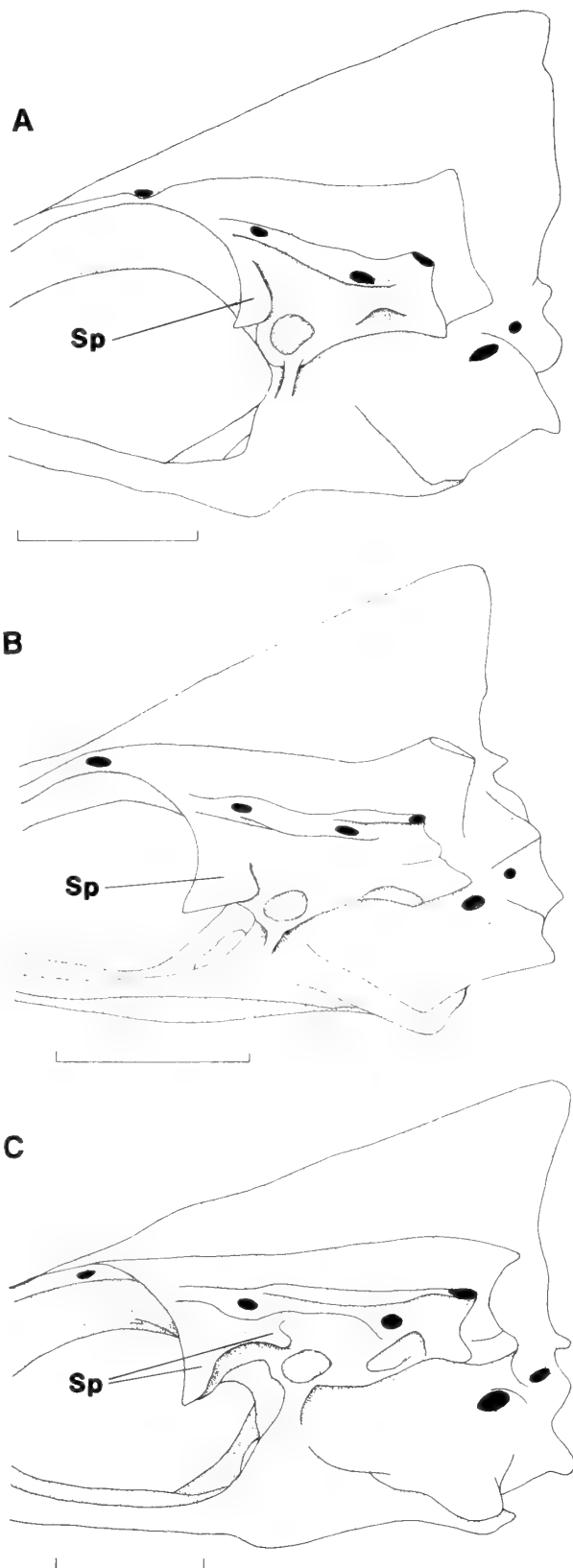


Fig. 3. Posterior portion of the neurocranium, in left lateral view, to show differences in the size of the sphenotic postorbital process (Sp.) in *Sargochromis*, *Chetia* and *Serranochromis*. A, *Sargochromis carlottae* (RUSI: 31204, 89 mm S.L.); B, *Chetia brevis* (AMG: P1422, 90 mm S.L.) and C, *Serranochromis macrocephalus* (RUSI: 24175, 112 mm S.L.) Scale bar = 5 mm.

have examined from the Okavango swamp and river system in Botswana seems to indicate that such variation may occur. A soft margin, for example, was absent in specimens of *Serranochromis thumbergi* and *S. longimanus*, but is present in *S. macrocephalus*. From the same samples some individual variability was noted both in the extent of the granular area on the caudal field of flank scales below the upper lateral-line, and the presence or absence of a granular area in at least some scales above that line. Apparent interspecific variation is also seen in the extent and nature of cheek, opercular and interopercular squamation patterns. The value of these features as a basis for intrageneric classification has, however, yet to be tested on a wider geographical and taxonomic basis.

A feature of *Serranochromis*, *Sargochromis* and *Chetia* noted in an earlier paper (Greenwood, 1979), where it was ranked as an apomorphy, is a reduction in the maximum number of inner tooth rows in both jaws to a single or irregularly double series. The new species, *S. altus*, described by Winemiller & Kelso-Winemiller (1991), is exceptional in having as many as six rows anteriorly, reducing to a single or double row posteriorly (the figures adjusted from Winemiller & Kelso-Winemiller who include the outer tooth row in their counts). These authors also note that the number of inner rows increases with growth "... in all species of *Serranochromis* that we have examined. . .". Their list of study material indicates, however, that only one other species, *S. angusticeps*, was studied, and that the maximum number of inner or outer rows in that species is three. Since museum specimens are often not fully representative of a species' full size-range, the possibility of growth related changes in the number of tooth rows should perhaps be treated, for the moment, as an open question. In that connection, however, it should be noted that in *Sargochromis*, one species, *Sargo. thysi*, has four inner rows in both jaws at a size when only one or two rows are present in other congeneric species.

Another dental feature in *Serranochromis*, one also shared with *Sargochromis*, (and probably *Chetia*), is for the two median teeth in the outer row of the inner tooth series to be enlarged and displaced anteriorly (Greenwood, 1984: 216; also see figs 3 & 8 in Trewavas, 1964). Amongst the sample of *Serranochromis* specimens examined, which included all species of the genus except *S. altus*. (see p. 35, and Greenwood, 1979 & 1984 for additional material), such tooth displacement occurs in most species but not in all individuals of a species. Its frequency of occurrence is lower in *Sargochromis* than in *Serranochromis*, and the condition is known from only one *Chetia* species (*C. gracilis*; see below and p. 39). Because of this inconstancy in its expression I would now consider the character more in the nature of a trend, albeit a derived one, rather than the trenchant synapomorphy recognised earlier (see Greenwood, 1984: 216).

A revised generic diagnosis for *Serranochromis* is given on p. 42, and the possible relationships of the genus are discussed on p. 40. To the list of included species published in Greenwood, 1979 (pp. 302–303) must be added *S. altus* Winemiller & Kelso-Winemiller (1991) from the Zambezi system.

Little need be added to previous accounts of the genus *Sargochromis*, type species *Paratilapia codringtoni* Blgr., 1908 (see Greenwood, 1979; 1984, in both papers the taxon treated as a subgenus) except to note that the species described as *Serranochromis* (*Sargochromis*) *gracilis* Greenwood (1984) from the Cunene river, is now considered to be a member of the genus *Chetia* (see p. 39). The transfer of this

species reduces to two the number of *Sargochromis* species having, relative to other congeneric taxa, slender lower pharyngeal bones with few and only partially molariform teeth, viz. *Sargochromis greenwoodi* (Bell-Cross) and *Sarg. coulteri* (Bell-Cross). The latter species, however, appears to show considerable variability in these features, with some individuals having noticeably coarser lower pharyngeal bones than do others, a feature invariably correlated with an increased number of molariform teeth (Greenwood, 1984: 217–221). As was discussed in that paper, the species level taxonomy of *Sargochromis* is far from satisfactory, so this seemingly intraspecific variability should only be accepted with some reservation (see also Greenwood, 1965 and Hoogerhoud, 1986).

In lacking a pronounced ventral expansion of its sphenotic postorbital process (see p. 37), the neurocranium in *Sargochromis* is immediately distinguishable from that of *Serranochromis* (see Fig 3; also comments in Greenwood, 1979: 303, and figs 13 & 16).

A list of *Sargochromis* species is given in Greenwood, (1979, pp. 304–305), and a revised generic diagnosis on p. 42 below.

The genus Chetia Trewavas, 1961

TYPE SPECIES: *Chetia flaviventris* Trewavas, 1961.

It has not proved possible to formulate a trenchant generic definition for *Chetia* since the taxon has yet to yield a single diagnostic autapomorphy. Its definition, therefore, is based on, as it were, negative features, namely those which exclude the five member species from inclusion in any of the three other serranochromine genera, especially *Serranochromis* with which *Chetia* has the greatest superficial and some detailed similarity. Thus, although *Chetia* shares with *Serranochromis* the apomorphy of two postorbital scale rows (see p. 36), a high number of caudal vertebrae (15–17, modes 16 or 17) and an increased number of circumpeduncular scales (18 or 20, rarely 16), it does not share with *Serranochromis* apomorphies of an increased number of abdominal vertebrae, (and as a consequence, an increase in the total number of vertebrae), nor the increased lateral-line scale count of that genus (35–41, a character probably correlated with the increased number of vertebrae). Neither do the two genera share the autapomorphic dental character of *Serranochromis*, namely the development of a totally unicuspid jaw dentition at a very small size; i.e., at some length, yet to be determined, less than 29 mm S.L.; see Greenwood, (1979: 300).

On the basis of that analysis, the simplest diagnosis for *Chetia* is: a *Serranochromis* lacking the apomorphic features of that genus (see also Greenwood, 1992: 49–50 and p. 43 below).

At the time of my earlier generic review (Greenwood, 1979), *Chetia* comprised two species, namely the type, *Chetia flaviventris*, and *Chetia brevis*, Jubb, 1968; the species coming from the Limpopo and Incomati river systems of South Africa respectively.

Based on Jubb's original description together with an examination of the holotype and two other *Chetia brevis* specimens, I excluded, in my 1979 paper, the species from *Chetia* and placed it, as *incertae sedis*, in the genus *Astatotilapia* (Greenwood, 1979: 284 & 307). That decision was based on three supposed features of *C. brevis*. (i) Jubb's (1968) description of the anal fin markings as ocelli, together with

his and my personal observations of their large size and restricted number (3 or 4) as compared with the small and numerous anal spots in other serranochromines (see p. 34), especially *Chetia flaviventris*. (ii) Jubb's (*op. cit.*) statement that the scales are ctenoid, and its implication that such scales are the predominant form. (iii) The presence of bicuspid teeth in the outer oral tooth rows of some specimens more than 100 mm S.L., contrasting with the situation in *Chetia flaviventris* where, on the information then available, few bicuspid teeth were thought to be present in fishes 71–85 mm S.L., and only unicuspid teeth occurred in specimens above that length.

Having now been able to examine colour-transparencies of live *C. brevis*, it is clear that the anal spots are not true ocelli (as defined on p. 34), but are large versions of the maculae found in other serranochromines, including *Chetia flaviventris*. The taxonomic significance to be attached to their large size, and small number, cannot yet be assessed. However, a wide size-range of anal maculae, their size negatively correlated with their number, occurs in the monotypic serranochromine genus *Pharyngochromis*, some individuals of which have spots as large as those in *Chetia brevis*.

The larger collection of *C. brevis* specimens now available, together with a re-examination of the entire type series, shows that Jubb's blanket description of the scales as ctenoid is somewhat misleading. As in *Chetia flaviventris*, the scales of *C. brevis* are cycloid above the lateral-line, and mostly cycloid below that level. A variable number, usually small, of ctenoid scales is present anteriorly on the flanks, such scales being most numerous in fishes less than 80 mm S.L. In other words, the same pattern as occurs in *Chetia flaviventris* is also found in *C. brevis*.

An examination of larger samples of both *C. flaviventris* and *C. brevis* also revealed that bicuspid teeth can be present in individuals of *C. flaviventris* up to a standard length of 90 mm, and that true unicuspid teeth as well as very weakly shouldered (almost unicuspid) teeth occur in *C. brevis* specimens between 80 and 90 mm S.L. This situation severely weakens my third reason (see above) for excluding *C. brevis* from the genus *Chetia*.

Furthermore, the presence of two vertical rows of postorbital scales in both *Chetia brevis* and *C. flaviventris* (see p. 36), a feature previously overlooked by all workers, provides additional evidence for returning the species 'brevis' to the genus in which it was originally, and I now acknowledge correctly placed by Jubb (1968).

Since 1979 another two species have been included in the genus, namely the taxon *Chetia mola* described by Balon & Stewart (1983) from the Zaire river system, and *Haplochromis welwitschi* (Blgr.) from Angola (see Greenwood, 1979 & 1984).

Chetia mola differs from all other congeneric species in having a greatly enlarged lower pharyngeal bone with a heavily molarized dentition (see fig. 12 in Balon & Stewart 1983), a type of pharyngeal mill more usually associated with species of *Sargochromis*. However, unlike members of that genus, *C. mola* has a double or sometimes triple row of postorbital scales, and a lower number of abdominal vertebrae.

To the existing four species of *Chetia*, I would now add a fifth, a species from the Cutato river, Angola, originally described (Greenwood, 1984) as *Serranochromis* (*Sargochromis*) *gracilis*. The reasons for this transfer are the double row of postorbital scales in 'gracilis', the persistence

of compressed, bi- and weakly bicuspid teeth in the outer tooth row of both jaws in specimens over 100 mm S.L. and of tricuspid teeth in the inner tooth rows in such individuals (see Greenwood, 1984: 227, and above), and the presence of only 15 abdominal vertebrae, a combination of derived and plesiomorphic characters not occurring in any known *Sargochromis* or *Serranochromis* species.

On the basis of comparisons with the few specimens available, *Chetia gracilis* (n=2) differs from the only other *Chetia* species recorded from southwestern Africa, *C. welwitschi* (n=5), in having a narrower interorbital width (18.2–18.6 cf 21.0–23.3% of head length in *C. welwitschi*), a larger eye (25.0–25.6, cf 18.6–22.25% head; the effects of allometry are unlikely to account for this difference since the two samples overlap in the size range of individuals represented), and a shallower cheek (22.7–23.3 cf 32.0–33.3% head). The lower pharyngeal bone in *C. gracilis* is somewhat stouter, and its median teeth coarser than in *C. welwitschi* (cf figs 19 & 20 in Greenwood, 1984).

In its morphometric and meristic features, *C. gracilis* closely resembles *C. flaviventris* and *C. brevis*, species respectively from the Limpopo and Incomati river systems in South Africa. From *Chetia brevis*, *C. gracilis* is distinguished by its narrower interorbital width (18.2–18.6 cf 23.0–26.0% head length), and from *C. flaviventris*, especially when specimens of approximately the same size are compared, by its shallower cheek (22.7–23.3 cf 25.5–33.6% head). It also seems likely that, when the effects of allometric growth are taken into account, the eye diameter is greater in *C. gracilis* than in *C. flaviventris*. The teeth in the median row of the lower pharyngeal bone of *C. gracilis* are coarser and stouter than those of *C. flaviventris*, in that respect being more like the teeth in *C. brevis* (cf fig. 19 in Greenwood, 1984, fig. 19 in Greenwood, 1974, and fig. 4B in Jubb, 1968).

Regrettably, apart from *Chetia flaviventris* (see du Plessis & Groenewald, 1953; Trewavas, 1961) and *C. mola* (see Balon & Stewart, 1983; fig. 10b) little or nothing is known about the live coloration of the other *Chetia* species.

A revised generic diagnosis for *Chetia* is given on p. 43.

Included species:

Chetia flaviventris Trewavas, 1961. Limpopo river system.

Chetia brevis Jubb, 1968. Incomati river system

Chetia mola Balon & Stewart, 1983. Luongo river, Zaire system.

Chetia welwitschi (Boulenger), 1898. Cunene and Zaire river drainage systems, Angola (see Greenwood, 1979).

Chetia gracilis (Greenwood), 1979. Cutato river (Cubango drainage system), Angola.

The genus *Pharyngochromis* Greenwood, 1979.

TYPE SPECIES: *Pelmatochromis darlingi* Boulenger, 1911.

A detailed revision of this monotypic genus, together with an annotated synonymy, has been published recently (Greenwood, 1992). Three nominal species all classified in the genus *Haplochromis* since Regan's revision of 1922 (or in one case, *Pharyngochromis*), viz. *Pelmatochromis darlingi* Boulenger, 1911; *Chromis jallae* Boulenger, 1896, and *Pelmatochromis multiocellatus* Boulenger, 1913, are now treated as junior synonyms of the single *Pharyngochromis* species, *P. acuticeps* (Steindachner) 1866.

There are some indications that *P. acuticeps* could be

considered either as a superspecies composed of several topospecies or as an assemblage of evolutionary species, but no clear-cut features allowing a formal taxonomic division of the taxon can be identified (see Discussion in Greenwood, 1992).

Anatomically and morphologically, *Pharyngochromis* is the least derived member of the serranochromines. Its sole autapomorphic feature is the higher position occupied by the posterior scales of the upper lateral-line series relative to the base of the dorsal fin (see Greenwood, 1992). The last five to seven (rarely four or eight) pored scales in that series are separated from the dorsal fin base by only one large and one much smaller scale. In the other serranochromine genera only the last one or two pored scales are separated from the fin base in this way, the other posterior scales having at least two large scales of equal size interposed between them and the fin base (see Greenwood, 1979 & 1992).

In most *P. acuticeps* specimens (from all localities) the lower pharyngeal bone is slightly enlarged, and some of its median row teeth, which are always coarser than their lateral congeners, have molariform or submolariform crowns (Greenwood, 1992, fig. 7). There is, however, considerable individual variability in the degree to which this bone is enlarged and its teeth are molarized. In these respects, *P. acuticeps* resembles certain *Sargochromis* species, particularly *S. couleri* (Bell-Cross) and *S. greenwoodi* (Bell-Cross). But, since the two genera differ in several other features, I would consider this resemblance to be homoplastic and not, as Trewavas (1961: 9) suggested, one of phylogenetic significance.

If the serranochromines are a monophyletic lineage, (see p. 41) their recent common ancestor could well have resembled the extant *Pharyngochromis acuticeps*, except for the incipient hypertrophy of the pharyngeal jaws in the latter.

Pharyngochromis acuticeps has a very wide distribution which includes the Zambezi and Save-Runde river systems, the Okavango river and its delta swamps, Lake Calundo, the Lucala river (Quanza drainage) and some unidentifiable localities in Angola. Records of the species (as *Haplochromis darlingi*) from the Limpopo river system (Jubb, 1967, repeated in Greenwood, 1979) are now known to be erroneous and probably based on the misidentification of small *Chetia flaviventris* specimens.

A revised generic diagnosis of *Pharyngochromis* is given in Greenwood (1992:48) and on p. 42 below.

CONCLUSION

The phyletic relationships of the serranochromines

The difficulties encountered in determining both the inter- and intrarelations of these fishes were discussed in two previous papers (Greenwood, 1979 & 1992), as was Trewavas' earlier (1964) tentative scheme of their relationships. Basically the problem lay, and still lies, in establishing whether or not the group is of monophyletic origin.

One of the two features unifying the serranochromines, the non-ocellate anal fin markings, is probably a plesiomorphic character, perhaps representative of a stage in the evolution of true ocelli and one in which the markings, unlike true ocelli, are not confined to males (Greenwood, 1979; Oliver,

1984). However, the possible function of anal maculae as egg-dummies (*sensu* Wickler, 1962; 1963), or even if they play any part in reproductive behaviour (Hert, 1989), have yet to be determined. There is also the possibility that non-ocellar anal markings have evolved more than once within the haplochromine cichlids (*sensu lato*), as their presence in species of *Thoracochromis* (Greenwood, 1979, 1984) could suggest. (Alternatively, *Thoracochromis* and the serranochromines may be more closely related than other morphological and anatomical evidence would indicate.) In this context, Eccles & Trewavas' (1989: 27) observations on three species of the endemic Malawi genus *Aulonocara* are pertinent. One of these species has simple spots, a second has spots surrounded by a contrasting border, and the third no markings at all, although the fin has a pale border. Since *Aulonocara* has a number of distinctive anatomical autapomorphies, this situation certainly suggests that not only have different kinds of anal fin markings evolved more than once but have done so within a single genus.

Another aspect of the problem involving phylogeny and anal markings is Oliver's (1984: 108) suggestion that haplochromines with multiple non-ocellar spots, together with those having true ocelli, comprise a monophyletic assemblage whose members are more closely related to one another than to any species with what he considers to be the plesiomorphic condition of anal maculae, namely spots indistinguishable from those on the other unpaired fins, especially the dorsal fin. That hypothesis has yet to be tested by the identification of suitable congruent and derived features characterizing the two supposed lineages, and raises questions about the significance of the seemingly unique anal marking of *Pseudocrenilabrus* species (Greenwood, 1989).

All in all, the current evidence for anal fin markings being of value in reconstructing phylogenies is not encouraging, particularly at the taxonomic levels under consideration here. For that reason I cannot agree with Eccles & Trewavas' (1989) use of the feature as grounds for suggesting a close relationship between the fluviatile serranochromines and most of the endemic haplochromines of Lake Malawi. While agreeing that non-ocellar anal spots are plesiomorphic features, these authors believe that the absence of true ocelli in the two groups "...combined with the geomorphological history of the region ... may be accepted as evidence for the relationship of the Malawian group of species with the haplochromines of the Zambezi area" (*i.e.*, with *Serranochromis*, *Sargochromis* and *Pharyngochromis*; *Chetia* has not been recorded from the Zambesi system). Certainly the similarity in anal fin markings would seem to support the intuitive feeling that the two groups could be related (see p. 34), and thus encourage a search for other characters to confirm or refute that impression, but in itself I would not rate it as 'evidence'.

The second morphological character used to define the serranochromines, *i.e.* cycloid scales above the lateral line and a preponderance of such scales below that level, is, I would argue, a derived condition (Greenwood, 1979; see also Oliver, 1984; Lippitsch, 1991). Nevertheless, it is not clearly an autapomorphic feature of the serranochromines. For example, in the Lake Malawi haplochromines mentioned above, there is also a marked reduction in scale ctenoidy, but here, although scales above the lateral-line, like those in the serranochromines, are cycloid, the ctenoid scales occurring below that level are confined to the posterior part of the body and not the anterior part as in serranochromines. In a

phylogenetic context how are these similarities and differences, to be evaluated?

Again, a pattern of reduced ctenoidy like that in the serranochromines occurs in some but not all species of *Thoracochromis* (Greenwood, 1979; 291; 1984:192 & 200), a genus in which, apparently, there are both true ocellar and non-ocellate types of anal fin markings (see above), but with both kinds occurring only in males. Possibly the 'genus' *Thoracochromis* is polyphyletic and that some of its species should be included in the serranochromine assemblage. Here, as is so often the case, one is hampered both by a paucity of detailed information on live coloration and the relatively few specimens available for anatomical and morphological studies.

Another difficulty, linked with lack of information, lies in the possibility that further research could establish that there really is a close phylogenetic relationship between the serranochromines and certain haplochromines of Lake Malawi. In that eventuality, it is possible that the nearest relative of one or more of the fluviatile serranochromine taxa is to be found in the lake's fauna, thus rendering the serranochromines, as currently conceived, either a para- or a polyphyletic group.

Although at present the monophyly of the serranochromines cannot be established or refuted, it is possible to construct, on the basis of shared derived features, a tentative intragroup taxonomy.

As compared with *Pharyngochromis*, the genera *Chetia*, *Serranochromis* and *Sargochromis* all share two derived features (see Liem, 1991) associated with the upper jaw skeleton, viz an increase in the shank length of the maxilla relative to its pre-shank length, and an increase in the length of the alveolar process of the premaxilla relative to the length of the entire ascending process of that bone (see Methods). In *Pharyngochromis* the preshank portion of the maxilla is from 1.2–1.3 times longer than its shank length, whereas in *Chetia* and *Sargochromis* the two parts are of equal length (with, in some *Sargochromis* species the preshank portion slightly shorter) and in *Serranochromis* the shank is noticeably longer (as much as 1.3 times so). In *Pharyngochromis* the length of the alveolar process of the premaxilla's ascending process is 60–66% of the length of the entire ascending process; in *Sargochromis* it is from 69–76%, in *Chetia* 73–77% and in *Serranochromis* 73–83%.

Neither of these ratios, either inter- or intragenetically, appears to be influenced by the size of the 17 specimens examined, all in the size range 79–410 mm S.L. and representing ten species.

On the basis of those two characters, a *Pharyngochromis* and a *Chetia* – *Serranochromis* – *Sargochromis* subgroup can be recognised within the serranochromines. Both these derived features are the only ones shared by the three latter genera (the increased number of abdominal vertebrae used previously to unite *Sargochromis* and *Serranochromis* in a single genus [Greenwood, 1979] is now thought to be a homoplasy; see p. 37).

Chetia and *Serranochromis* both share three derived features not found in *Sargochromis* or in *Pharyngochromis* viz. (i) an increased modal number of caudal vertebrae (range 15–17, modes 16–17 in *Chetia*, and 15–18, modes 16 and 17 in *Serranochromis*) compared with *Sargochromis* (range 12–16, modes 14 and 15) and *Pharyngochromis* (range 14–16, mode 15). (ii) Two or more vertical rows of postorbital scales (cf a single row in *Sargochromis* and *Pharyngochromis*, see p. 36). (iii) An increased number of scale rows around the caudal

peduncle, i.e. 18–20, rarely 16, compared with 16–18 rarely 15, (mode 16), in *Sargochromis*, and 15 or 16 (mode 15) in *Pharyngochromis*.

On the basis of those three derived characters, and using the term 'sister taxon' without any phylogenetic implications, then, within the serranochromines, *Pharyngochromis* is the sister taxon to the group *Sargochromis*, *Chetia* and *Serranochromis*, and within that latter group, *Sargochromis* is the sister taxon of *Serranochromis* and *Chetia* combined.

That scheme bears, in broad outline, a close resemblance to Trewavas's (1964) diagram suggesting the interrelationships of *Serranochromis*, a scheme based essentially on lateral-line and dorsal fin ray counts (which may, of course, be correlated, in part, with the vertebral counts used here) and certain characteristics of the pharyngeal jaws.

When comparing the two schemes, allowances must be made for the fact that two of Trewavas' *Haplochromis* species (*lucullae* and *darlingi*) are now treated as synonyms of *Pharyngochromis acuticeps* (Greenwood, 1992), that the status of *H. angolensis*, *H. humilis* and *H. toddi* is uncertain or unknown (Bell-Cross, 1975; Greenwood, 1979), and that *H. welwitschi* is now considered to be a species of *Chetia* (see p. 39). Also, the two *Haplochromis* species, *mellandi* and *frederici*, placed in limbo between the genera *Haplochromis* and *Sargochromis* in Trewavas' diagram, are now included in *Sargochromis* (Bell-Cross, 1975; Greenwood, 1979 and above p. 37), as is *Haplochromis carlottae*.

Trewavas (*op. cit.* 9–10) superimposed on her diagram a tree indicating the possible phylogenetic relationships of the taxa, both inter- and intragenetically. It is here that our views would not coincide, mainly because I do not think there is the evidence, based on cladistic methodology, to justify the relationships proposed, even at an intergeneric level (see p. 40). Certainly there are no features justifying Trewavas' (*op. cit.* 10) suggestion that *Serranochromis* is a diphyletic and gradal taxon or that a cladal grouping would recognise *Chetia*, *Serranochromis robustus* and *S. thumbergi* on the one hand, and *Chetia welwitschi* (Trewavas' *Haplochromis welwitschi*), and the remaining *Serranochromis* species on the other. Nor can I accept Trewavas' uncertainty about the separation of *Sargochromis codringtoni*, *mellandi*, *carlottae* and *greenwoodi* (as *Haplochromis frederici* in her scheme; see Bell-Cross, 1975) from the 'Haplochromis' (i.e. *Pharyngochromis*,) root of her tree (see Greenwood, 1979, 1992 and above). A truly phylogenetic assessment of the groups' relationships must, as discussed on p. 36, await the results from further and preferably multidisciplinary research into the systematics of all the serranochromine species, and those many Malawi species that Eccles & Trewavas (1989: 21) have placed in their *Pharyngochromis* – *Chetia* – *Serranochromis* group.

Generic key and diagnoses

A single row of scales between the posterior orbital margin and the vertical limb of the preoperculum A
Two or more scale rows between the posterior orbital margin and the vertical limb of the preoperculum B

A. Last 2 or 3 pored scales in the upper lateral-line series separated from the dorsal fin base by not less than two scales of approximately equal size A(i) *Sargochromis*
Last 5 to 7 (rarely 4 or 8) pored scales in the upper lateral line separated from the dorsal fin base by one large and one small scale A(ii) *Pharyngochromis*

A(i):

Abdominal vertebrae [15] 16–18 [19], modes 16 and 17; caudal vertebrae 12–16, modes 14 and 15; total number of vertebrae 28–32 (mode 31).

Dorsal fin with 13–16, modes 15 and 16, spinous rays and 11–16, modes 12 and 13, branched rays. Anal fin with 3 spines and 8–11, mode 9, branched rays. Caudal fin truncate, subtruncate or almost rounded.

Scales in the lateral series 28–34, modes 30 and 31. Cheek with 3–6 horizontal rows. [15] 16–18, mode 16, scales around the caudal peduncle.

Gill-rakers in the outer series on the first ceratobranchial 9–15, modes 12 and 13.

Outer series of teeth in both jaws composed mainly of unequally bicuspid teeth in fishes <150 mm S.L., but predominantly of unicuspid teeth in larger specimens. Inner series of jaw teeth, except in one species, arranged in a single or double series anteriorly and anterolaterally, reducing to a single row posterolaterally; in the exceptional species there are 4 rows anteriorly and anterolaterally, and a single row posterolaterally.

Pre-shank length of the maxilla equal to, or slightly shorter than the shank-length (see p. 34). Height of the premaxillary alveolar process 69–76% of the height of the entire ascending process (see p. 35). For comments on neurocranial morphology and other osteological features (including the lower pharyngeal bone and its dentition, see text and figures in Bell-Cross (1975) and Greenwood (1979: 303–305, figs. 16–18; and 1984: 216–225, figs. 12–17).

Lower pharyngeal bone hypertrophied in the majority of species, greatly so in some, but only slightly enlarged in two species. The extent and degree to which the dentition of this bone is molarized is positively correlated with the degree of the bone's hypertrophy. In species with slightly enlarged bones only a few molar-like or submolariform teeth are present, and are confined to the median tooth rows. The ventral outline of the bone's anterior keel is almost straight and rarely extends below a horizontal drawn through the deepest point on the bone's ventral surface below the dentigerous area. In specimens with a greatly enlarged lower pharyngeal bone, however, the ventral margin of the keel extends a little below that level (see figs 12–17 in Greenwood, 1984).

Anal fin spots small and numerous (as many as 40). *Sargochromis*

A(ii):

Abdominal vertebrae [13] 14 or 15 [16], mode 14; caudal vertebrae 14–16, mode 15; total number of vertebrae 28–31, mode 30.

Dorsal fin with 14–16, mode 15, spinous rays and [10] 11–13 [14] branched rays. Anal fin with 3 spines and 8 or 9 branched rays (no distinct modal number). Caudal fin distinctly truncate, subtruncate or almost rounded.

Scales in the lateral series [30] 31–36, mode 33, modal range 32–34. Cheek with [3] 4–6 horizontal rows. 15, rarely 16, scales around the caudal peduncle.

Gill-rakers in the outer row on the first ceratobranchial 7–12, modes 9 and 10.

Outer series of jaw teeth composed of unequally bicuspid teeth in fishes <80 mm S.L., although some unicuspid teeth can be found in larger fishes within that length range. Unicuspid teeth become the predominant form in fishes >90 mm S.L. Inner series of teeth, in both jaws, arranged in 1–3 rows anteriorly

and anterolaterally, reducing to a single row posterolaterally. The number of inner rows anteriorly appears to be positively correlated with an individual's size.

Pre-shank length of the maxilla clearly greater than the shank length (see p. 34), i.e. about 1.2–1.3 times longer. Height of premaxillary alveolar process 60–66% of the height of the entire ascending process. For comments on neurocranial form and other osteological features, see Greenwood (1992).

Lower pharyngeal bone in most individuals showing a slight degree of hypertrophy. In specimens over 50 mm S.L., the median rows of lower pharyngeal teeth are composed of noticeably coarser teeth than those situated laterally, and some can have submolariform crowns; the degree of molarization is most marked in fishes over 100 mm S.L. Irrespective of the degree to which the lower pharyngeal bone is enlarged, its anterior keel is deep, with a curved ventral outline whose deepest point lies below a horizontal drawn though the deepest point of the ventral surface underlying the dentigerous part of the bone (cf *Sargochromis* above); see fig. 7, Greenwood, 1992.

Anal fin spots of variable size and number, from as few as 3 or 4 large spots to as many as 19 small ones *Pharyngochromis*.

B. 16–18 (rarely 15 or 19) abdominal vertebrae; inner and outer rows of jaw teeth composed entirely or mostly of unicuspid teeth in fishes over 30mm S.L. (and possibly in smaller individuals as well) **B(i)** *Serranochromis*
14 or 15 abdominal vertebrae; many bicuspid (or weakly bicuspid) teeth present in the outer tooth rows of both jaws in fishes as large as 80 mm S.L. **B(ii)** *Chetia*

B(i)

Abdominal vertebrae [15] 16–18 [19], modes 16 and 17; caudal vertebrae [15] 16–18, modes 16 and 17; total number of vertebrae 31–36 (no distinct modes).

Dorsal fin with 13–18, modes 15 and 16, spinous rays, and 13–16, modes 14, 15 and 16, branched rays. Anal fin with 3 spines and 9–13, modes 10 and 11, branched rays. Caudal fin subtruncate or almost rounded.

Scales in the lateral series [34] 35–41, no distinct modes. Cheek with 3 (rarely) to 11 horizontal rows (modally 5–9 rows). 18–20 scales around the caudal peduncle (no distinct mode).

Gill-rakers in the outer series on the first ceratobranchial [8] 9–13, modes 10, 11 and 12.

Outer and inner series of jaw teeth composed of unicuspid teeth in specimens over 30 mm S.L. Inner series of both jaws, in all but one species, arranged in a single or double row (rarely 3 rows) anteriorly and anterolaterally, and a single row posterolaterally. In the exceptional species there are as many as six rows anteriorly and anterolaterally, reducing to a single or double row posterolaterally.

Pre-shank length of the maxilla shorter than its shank-length (see p. 34), which is ca 1.2–1.3 times longer than the pre-shank portion. Height of the premaxillary alveolar process 73–82% of the height of the entire ascending process (see p. 34). For comments on the neurocranium and other osteological features see Greenwood (1979: 299–302; figs. 13–15) and Trewavas (1964).

Lower pharyngeal bone slender, its dentigerous surface elongate and narrow (see figures in Trewavas, 1964, and Greenwood, 1979). No molariform pharyngeal teeth; even

those teeth in the median rows are only a little coarser than the other and fine teeth on the bone.

Anal fin spots small and numerous (as many as 40) *Serranochromis*

B(ii):
Abdominal vertebrae 14 or 15 (no distinct mode); caudal vertebrae 15–17, modes 16 and 17; total number of vertebrae 30–32, mode 31.

Dorsal fin with 14 or 15, mode 15, spinous rays and 10–13, modal range 11 or 12, branched rays. Anal fin with 3 spines and 7–10 branched rays (no distinct mode). Caudal fin truncate to subtruncate.

Scales in the lateral series 32–35, modal range 32–34. Cheek with 4–6, modes 5 and 6, horizontal rows; 18 or 20 (rarely 16) scales around the caudal peduncle.

Gill rakers in the outer series on the first ceratobranchial 9–11, modes 10 and 11.

Outer series of teeth in both jaws composed mainly of unequally bicuspid, but with a few unicuspid or weakly shouldered bicuspid present, in fishes < 80 mm S.L.; however, in some specimens of *Chetia flaviventris*, unicuspid predominate in fishes in the upper part of that size-range. In specimens >100 mm S.L. the outer teeth are predominantly unicuspid, with a few very weakly shouldered bicuspid also present. Inner tooth rows of both jaws arranged in a double series anteriorly and anterolaterally, reducing to a single row laterally and posteriorly. In one species (*Chetia gracilis*) at least some specimens have the two anterior median teeth in the outer row of inner teeth enlarged and displaced anteriorly relative to the other teeth in that row.

Pre-shank length of the maxilla equal to its shank length (see p. 34). Height of the premaxillary alveolar process 73–77% of the height of the entire ascending process (see p. 35).

Except in one species, the lower pharyngeal bone is not enlarged, and the median tooth rows are composed of bicuspid teeth only a little coarser than their lateral congeners. In the exceptional species, *C. mola* (see Balon & Stewart, 1983; fig. 12) the bone is greatly hypertrophied and massive, with all but a few of its laterally situated teeth enlarged and molariform or submolariform.

Anal fin spots usually small and fairly numerous (7–15) but in one species, *C. brevis*, there are only 3 or 4 large spots. *Chetia*

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A revision of *Danielssenia* Boeck and *Psammis* Sars with the establishment of two new genera *Archisenia* and *Bathypsammis* (Harpacticoida: Paranannopidae)

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SYNOPSIS. *Archisenia* gen. nov. is proposed to accommodate the *sibirica*-group of the genus *Danielssenia* Boeck, 1872. Re-examination of Alaskan material of *D. stefanssoni* Willey, 1920 has shown the latter species to be a junior synonym of *D. sibirica* Sars, 1898, the type and only species of the new genus.

Danielssenia robusta Sars, 1921 and *Fladenia intermedia* (Wells, 1965) are synonymous and consequently *F. robusta* comb. nov. becomes the type species of the genus *Fladenia* Gee & Huys, 1990. *Danielssenia similis* Chislenko, 1971 is regarded as *species inquirenda* and the genus *Danielssenia* is redefined from the type species *D. typica* Boeck, 1872, and two other species (*D. quadriseta* Gee, 1988 and *D. reducta* Gee, 1988).

The status of *D. fusiformis* (Brady, 1880) nec Sars (1910) is reconsidered and as a result the genus *Sentirenia* Huys & Gee, 1992 is relegated to a junior synonym of *Jonesiella* Brady, 1880 which is reinstated to accommodate *J. fusiformis* Brady, 1880 and *J. eastwardae* (Coull, 1971) comb. nov.

Psammis borealis Klie, 1939 is removed from the genus *Psammis* Sars, 1910 but retained in the Paranannopidae as *species incertae sedis*. *P. longifurca* Bodin, 1968 is transferred from *Psammis* to *Bathypsammis* gen. nov. The genus *Psammis* is redefined on the basis of the type species *P. longisetosa* Sars, 1910, and *P. longipes* Becker, 1974.

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A detailed redescription of *A. sibirica* and new illustrations of *D. typica*, *P. longisetosa*, *P. longipes* and *B. longifurca* are provided.

Intersexuality in copepods and the possible phylogenetic relationships of *Danielssenia*, *Psammis*, *Fladenia*, *Archisenia* gen. nov. and *Bathypsammis* gen. nov. are briefly discussed.

A key to the genera of the Paranannopidae is presented.

INTRODUCTION

Throughout its taxonomic history up to the late 1980s, the genus *Danielssenia* Boeck, 1872 has served as a repository to accommodate different kinds of 'tachidiid' harpacticoid copepods, in so far that the distinction between this genus and *Psammis* Sars, 1910 almost became no longer tenable (Wells, 1965, 1967). Gee (1988a) pointed out that differences in mandibular gnathopod structure, possibly reflecting different diets, could indicate that both genera are trophically isolated, but admitted that perhaps more solid morphological evidence is necessary to maintain generic distinction.

The criteria applied by most workers to allocate newly discovered species to *Danielssenia* generally had no phylogenetic significance as they were mainly based on plesiomorphic character states (i.e. P1 not modified) which are diagnostic of a wider group of families. Virtually no effort has been made to correctly assess the sexual dimorphism on the swimming legs and very little information on detailed mouthpart structure has been documented. Both categories of characters have nevertheless proved to hold a high phylogenetic information content that can be used to determine relationships within the *Danielssenia*-*Psammis* core group of genera (Gee & Huys, 1990, 1991; Huys & Gee, 1992, in press).

The impact of Lang's (1944, 1948) classification of the Tachidiidae also caused people to lose sight of the relationships of this core group with taxa beyond the family boundaries. The fact that his artificial subdivision into three subfamilies constrained the development of alternative phylogenetic scenarios for a long time is illustrated by the ongoing discovery and description of numerous new species of *Paranannopus* Lang, 1936 (placed in the Cletodidae and subsequently in the Paranannopidae) and *Danielssenia*

(placed in the Thompsonulinae, Tachidiidae) in the post-Langian era without any recognition of the close relationship between these two taxa. Huys & Gee (1990) inevitably had to break down the concept of the Thompsonulinae before they could re-allocate the 'danielsseniid genera' to the Paranannopidae. This group of genera essentially represents the continental shelf lineage of the family with a few species that secondarily explored deeper habitats (e.g. *Leptotachidia iberica* Becker, 1974). Its affinity to the predominantly deepwater group, containing *Paranannopus* and *Cylindronannopus* Coull, 1973, has recently been supported by the redescription of *Fladenia* Gee & Huys, 1990, a possible 'missing link' between both lineages (Gee & Huys, 1990).

This paper is the final contribution to a revision of the genus *Danielssenia*, including the allocation of the *sibirica*-group to a new genus *Archisenia*, thus reducing the number of species previously referred to the genus from 14 to four (Table 1). It also presents a revision of the other major genus *Psammis*, resulting in the proposal of a new genus *Bathypsammis*. With the revision of these taxa the establishment of novel genera draws to a close and, accordingly, a key to genera of the Paranannopidae is presented.

MATERIALS AND METHODS

Before dissection, the habitus was drawn and body length measurements were made from whole specimens temporarily mounted in lactophenol. Specimens were then dissected in lactic acid, the parts mounted in lactophenol and the preparations sealed with glyceel® (BDH Chemicals Ltd, Poole, England). All drawings of the specimens were prepared using a camera lucida on a Leitz Dialux 20 or Leitz Diaplan

Table 1 Re-allocation of species previously referred to *Danielssenia* Boeck, 1872.

Species previously referred to <i>Danielssenia</i>	Current status	Reference
<i>typica</i> Boeck, 1872	<i>Danielssenia typica</i> Boeck, 1872	Gee (1988)
<i>fusiformis sensu</i> (Sars, 1910)	<i>Danielssenia typica</i> Boeck, 1872	Gee (1988), present account
<i>quadriseta</i> Gee, 1988	<i>Danielssenia quadriseta</i> Gee, 1988	Gee (1988)
<i>reducta</i> Gee, 1988	<i>Danielssenia reducta</i> Gee, 1988	Gee (1988)
<i>similis</i> Chislenko, 1978	<i>Danielssenia similis</i> Chislenko, 1978 [<i>sp. inq.</i>]	present account
<i>sibirica</i> Sars, 1898	<i>Archisenia sibirica</i> (Sars, 1898) comb. nov.	present account
<i>stefanssoni</i> Willey, 1920	<i>Archisenia sibirica</i> (Sars, 1898) comb. nov.	Gee (1988)
<i>fusiformis</i> Brady, 1880	<i>Jonesiella fusiformis</i> Brady, 1880	present account
<i>perezi</i> Monard, 1935	<i>Jonesiella fusiformis</i> Brady, 1880	present account
<i>paraperezi</i> Soyer, 1970	<i>Jonesiella fusiformis</i> Brady, 1880	Huys & Gee (1992), present account
<i>eastwardae</i> Coull, 1971	<i>Jonesiella eastwardae</i> (Coull, 1971) comb. nov.	Huys & Gee (1992), present account
<i>robusta</i> Sars, 1921	<i>Fladenia robusta</i> (Sars, 1921) comb. nov.	present account
<i>intermedia</i> Wells, 1965	<i>Fladenia robusta</i> (Sars, 1921) comb. nov.	Gee & Huys (1988), present account
<i>spinipes</i> Wells, 1967	<i>Afrosenia spinipes</i> (Wells, 1967)	Huys & Gee (in press)
<i>minuta</i> Coull, 1969	<i>Sentiropsis minuta</i> (Coull, 1969)	Huys & Gee (in press)

differential interference contrast microscope. The terminology for body and appendage morphology is according to Huys and Boxshall (1991). Abbreviations used in the text and figures are P1–P6 for thoracopods 1–6; exp(enp)-1 (-2,-3) to denote the proximal (middle, distal) segment of a ramus. Body length was measured from the base of the rostrum to the posterior margin of the anal somite.

SYSTEMATICS

Family Paranannopidae Por, 1984

Genus *Archisenia* gen. nov.

SYNONYMY. *Danielssenia* Boeck, 1872 (part).

DIAGNOSIS. Paranannopidae. Body large, slightly fusiform and dorso-ventrally flattened. Rostrum not hyaline, with 2 pairs of small sensillae. Somatic hyaline frills minutely dentate. Female genital double-somite with lateral and ventral sub-cuticular ridge marking original segmentation; genital field with minute copulatory pore and sinusoidal copulatory duct leading to transverse seminal receptacle partly located anterior to genital slit; P6 with 1 outer plumose seta and 2 minute spiniform elements. Pseudopericulum hyaline with dentate margin. Caudal rami slightly divergent and slightly longer than broad. Female antennule 6-segmented; aesthetasc on segment 4; distal 2 segments with heavily pectinate spines. Antennary exopod 3-segmented with armature formula [2-1-3]. Mandibular coxa elongate, with blunt teeth on gnathobase; basis with 4 setae; endopod 1-segmented; exopod 2-segmented. Maxilliped subchelate with 1 large and 1 small seta on syncoxa; basis with naked seta on palmar margin, endopodal claw with 2 accessory setae. P1 exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod longer than exopod, 2-segmented, enp-2 4.5 times longer than broad, inner seta implanted medially. P2–P4 intercoxal sclerites with spinules or setules on distal margin; rami 3-segmented; exp-1 with inner seta; female P2–P3 enp-2 with small apophysis at outer distal corner. Armature formula of P1–P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.1.221
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

Female fifth pair of legs not fused medially; exopod and baseoendopod separate, each with 5 setae, inner seta on exopod well separated from remaining 4 setae.

Male with sexual dimorphism on antennule, P1, P2 endopod, P3 endopod, P5, P6 and in genital segmentation. Antennule 9-segmented, subchirocer; segment 6 very swollen, with aesthetasc. P1 inner basal spine less strongly developed, segments of rami more slender and spinule rows on outer margin of endopod much smaller. P2 enp-1 larger, with inner seta transformed into a non-articulating process; enp-2 without inner seta, outer distal corner attenuated into a long apophysis reaching far beyond the distal border of enp-3;

enp-3 with distal outer spine partially fused to segment, much shorter and stronger than in female, with spinules reduced to coarse teeth, other setae reduced in size. P3 enp-2 with inner distal corner slightly attenuated, outer distal corner attenuated into a hook-shaped apophysis. Fifth pair of legs fused medially; baseoendopod and exopod separate with 2 and 5 setae, respectively. P6 symmetrical, fused to somite, with 3 setae each.

TYPE SPECIES. As a result of the arguments and analysis put forward below we regard *D. stefanssoni* Willey, 1920 as a junior synonym of *D. sibirica* Sars, 1898 and therefore *A. sibirica* (Sars, 1898) comb. nov. is designated as the type species.

OTHER SPECIES. None.

ETYMOLOGY. The generic name is derived from the Greek prefix *archi*, meaning first in time and alludes to the primitive position in the family. Gender: feminine.

Archisenia sibirica (Sars, 1898) comb. nov.

SYNONYMY. *Danielssenia sibirica* Sars, 1898; *Danielssenia stefanssoni* Willey, 1920.

MATERIAL EXAMINED.

— National Museum of Natural History (Smithsonian Institution), Washington, D.C.: 8 ♀♀ and 1 ♂ from Point Barrow, Nuwuk Lake, Alaska, U.S.A.; collected by R. Lewis *et al.*, August 1 1960, bottom sample A974; identified as *D. stefanssoni* by M.S. Wilson; 1 ♀ dissected on 13 slides, 1 ♂ dissected on 7 slides, others preserved in alcohol: reg. no. USNM 204769.

— Naturhistoriska Riksmuseet, Stockholm: 1 ♀ and 1 ♂ from East Greenland, Barclay Bay; collected by Jespersen, July 14 1932; identified as *D. stefanssoni* by K. Lang; preserved in alcohol; reg. no. Cop. 31.

DESCRIPTION OF FEMALE. Body slightly dorso-ventrally flattened (as for male, Fig. 9B); length 0.97–1.242 mm (\bar{x} = 1.15 mm; n = 7); urosome clearly demarcated from prosome. Cephalothorax rounded anteriorly, widest near posterior margin. Rostrum (Fig. 2A) not hyaline; tapering anteriorly; with 2 pairs of sensillae. Free prosomites each with a dorsal row of spinules and some sensillae near posterior margin; hyaline frill of prosomites minutely dentate. All urosomites (Fig. 1A–B) with lateral row of spinules; first to third urosomites with dorsal row of spinules, 2 rows dorsally on genital somite; ventral spinule row on posterior border of genital double-somite and succeeding urosomites, slightly anterior to lateral rows. Genital double-somite (Fig. 1A–B) with lateral and ventral subcuticular ridge. Genital field (Fig. 1C–D) with minute copulatory pore posterior to genital slit; copulatory duct sinusoidal (Fig. 1D) leading to single, transversely elongate seminal receptacle located at level of genital slit; vestigial P6 with 1 plumose seta and 2 spinules (vestigial setae?); paired, blind ending, cuticular invaginations posterior to genital field (Fig. 1C). Hyaline frill of urosomites minutely dentate, that of penultimate somite extended to form pseudopericulum (Figs. 1B, 8C). Anal somite deeply incised. Caudal rami (Figs. 1E, 5F, 8C) tapering posteriorly, slightly longer than broad, with short spinule row medially on lateral margin and a latero-ventral spinule row on distal margin which also has a large pore near ventral outer corner (Fig. 1E); seta I minute (Fig. 5F); setae IV & V well

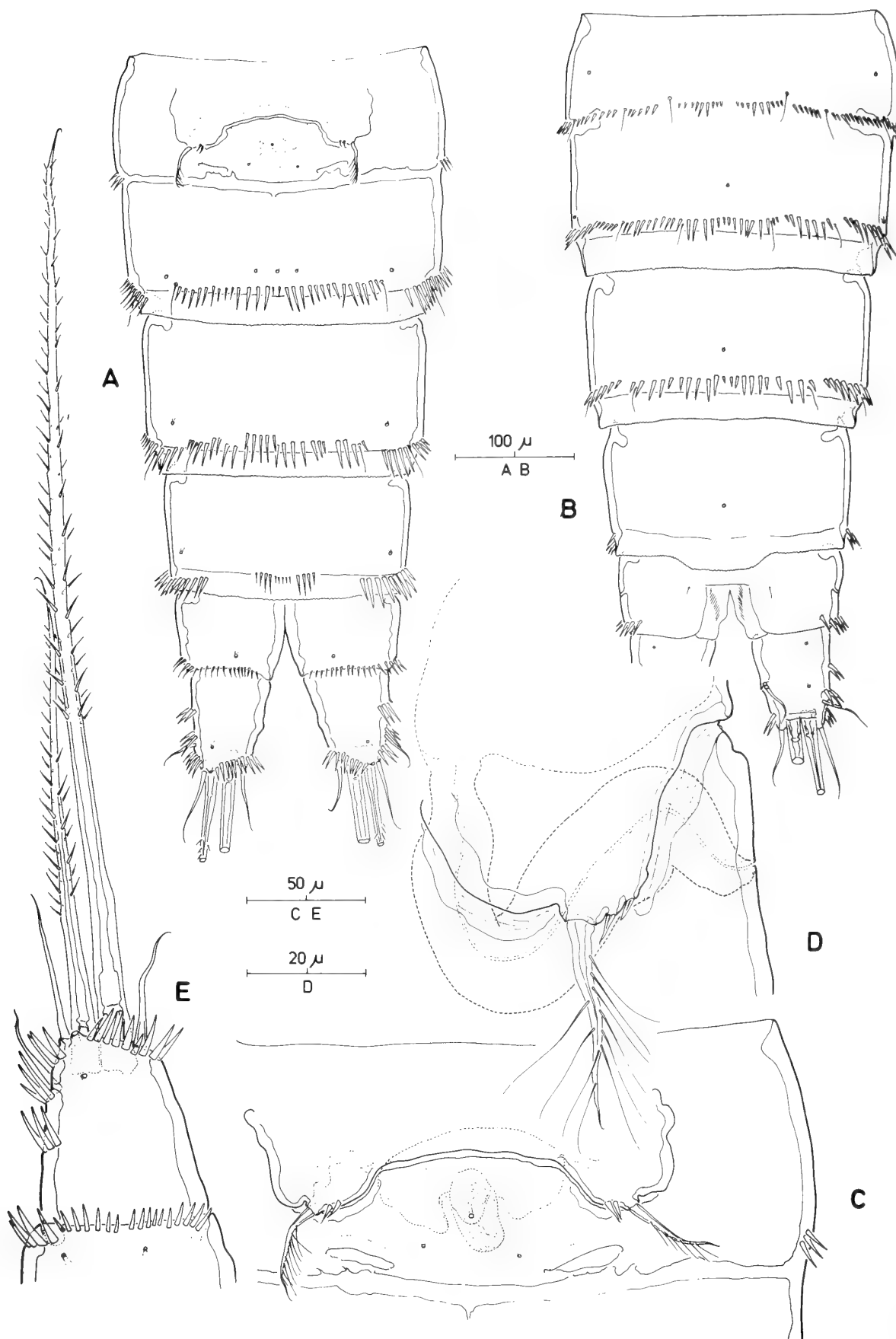


Fig. 1 *Archisenia sibirica* comb. nov. A, Female urosome (excluding P5-bearing somite), ventral view; B, same, dorsal view; C, female genital field, ventral view; D, same lateral view; E, caudal ramus, ventral view.

developed, spinulose in distal portion (Fig. 1E); seta VII tri-articulate (Fig. 8C).

Antennule (Fig. 2A–B) 6-segmented; segment 1 with 2 spinule rows on outer margin and a plumose seta at outer distal corner. Segment 2 with 5 pinnate and 1 naked setae on outer margin and 2 pinnate and 1 naked setae posteriorly directed on dorsal margin. Segment 3 with 2 pinnate and 6 naked setae at outer distal corner. Segment 4 with 6 naked setae and an aesthetasc. Segment 5 with 3 pectinate spines, 3 naked and 2 pinnate setae. Segment 6 with 1 pectinate spine and 7 naked setae.

Antenna (Fig. 2C–D). Coxa with a row of spinules proximally. Allobasis with long spinules at base of abexopodal, pinnate seta. Exopod 3-segmented with armature formula [2-1-3]; distal segment elongate with subterminal row of spinules. Endopod with 2 spinule rows on outer margin; 2 spines, a geniculate seta and a naked seta subdistally (Fig. 2C); distal margin with a pectinate spine, 4 geniculate setae, a small plumose seta (Fig. 2C) and a very small naked seta (Fig. 2D).

Mandible (Fig. 3A–B). Coxa (Fig. 3B) elongate, slender, with 2 median rows of spinules; gnathobase with bidentate and unidentate teeth and a pinnate seta at inner distal corner. Palp biramous. Basis (Fig. 3A) with patch of spinules medially and 4 pinnate setae on distal margin. Exopod 2-segmented; proximal segment with 2 pinnate setae laterally and a row of large spinules distally; distal segment with 3 apical setae. Endopod 1-segmented with 3 lateral and 6 distal setae.

Labrum (Fig. 3C) with numerous spinule rows near median distal margin of posterior face.

Maxillule (Fig. 3D). Praecoxal arthrite with 2 juxtaposed setae medially on anterior surface and 9 bidentate or pinnate spines and 1 naked seta on distal margin. Coxal endite with 5 armature elements on distal margin. Basal endite with 2 subdistal setae and 4 setae on distal margin. Rami 1-segmented and each with 3 setae.

Maxilla (Fig. 4B). Syncoxa with spinule row at outer proximal corner and with 3 endites each with 1 fused and 2 articulating pinnate spines. Allobasal endite with a fused pinnate claw, a pinnate spine and 2 setae. Endopod 1-segmented with a pinnate spine and 3 setae.

Paragnaths (Fig. 4A) well developed; with several rows of fine spinules laterally and medially; anterior face with coarse teeth.

Maxilliped (Fig. 4C). Syncoxa with numerous spinule rows, 1 large subterminal and 1 smaller terminal pinnate seta. Basis with row of spinules and a naked seta on palmar margin. Endopodal claw as long as basis, spinulose distally and with 2 accessory setae proximally.

P1 (Fig. 5A). Intercoxal sclerite rectangular with 2 groups of setules on each side. Coxa with rows of spinules on anterior face and outer margin. Basis with row of spinules on inner and distal margin and around base of inner pectinate spine (Fig. 1D) and outer pinnate seta. Exopod 3-segmented, each with row of spinules on outer margin, outer spines pectinate, distal outer spine on exp-3 longer than middle outer spine. Endopod longer than exopod, 2-segmented; proximal segment slightly longer than broad, distal segment about 4.5 times longer than broad, inner seta implanted medially.

P2–P4 (Figs. 6A, 7A, 8A). Intercoxal sclerite with row of spinules or setules on each side. Both rami 3-segmented, equal in length in P2 but with endopod shorter than exopod in

P3 and P4; all segments with rows of spinules on outer margin; P2 and P3 with a large spinule at base of each inner seta on enp-2 and -3. Exp-1 with inner seta; enp-2 with outer distal margin somewhat attenuated. Armature formula of swimming legs as in generic diagnosis.

Fifth pair of legs (Fig. 11D) not fused medially; exopod and baseoendopod separate. Baseoendopod with short row of spinules at base of exopod and setophore of outer seta; endopodal lobe well developed, tapering distally, with 5 pinnate setae, second outer seta longest. Exopod wider than long, boundary with baseoendopod straight, not reaching to distal margin of endopodal lobe; with 5 pinnate setae, 4 grouped together on distal outer margin and 1 well separated near inner distal corner.

DESCRIPTION OF MALE. As in female except for following characters.

Body (Fig. 9). Length 1.008 mm ($n = 1$); second and third urosomites not fused and ornamental spinules on urosome somewhat more robust (Fig. 11A).

Antennule (Fig. 10) 9-segmented, subchirocer with 6th segment very swollen, geniculation between 6th and 7th segments. Segmental fusion pattern: I, II, III–VIII, IX–XII, XIII, XIV–XX, XXI–XXIII, XXIV–XXV, XXVI–XXVIII. Armature formula: [1, 1, 11, 8, 1, 14+ae, 4, 3, 8]. Segment 6 very swollen with a complicated pattern of ridges and teeth on anterior surface (Fig. 10C–D). Segment 7 with 4 setae, 3 of which sagittiform, on anterior surface (Fig. 10E).

P1. Coxa with fewer spinule rows on anterior surface. Inner spine on basis without spinule row at base; inner spine less well developed and with finer spinules (Fig. 5E) than in female (Fig. 5D). Segments of both rami (Fig. 5B) more elongate than in female. Spinules on outer and distal margin of endopod segments much finer than in female, particularly on distal margin of enp-1 (Fig. 5C).

P2 (Fig. 6B–C). Basal pedestal and articulating surface of endopod enlarged. Enp-1 much larger than in female and inner seta transformed into a non-articulating process with a flagellate tip; outer spinules small. Enp-2 without inner seta or spinule row on outer margin; outer distal corner attenuated into an apophysis reaching well beyond the distal margin of enp-3. Enp-3 (Fig. 6C) reduced in size with no outer spinule row; outer distal spine shorter but stouter than in female with spinules reduced to coarse blunt teeth; terminal and inner setae also reduced in size compared to female.

P3 endopod (Fig. 7B–C). Enp-2 without outer spinule row; outer and inner distal corners much more attenuated than in female, apophysis at outer corner with hooked tip (Fig. 7C); inner seta much smaller than in female.

P5 (Fig. 11B). Baseoendopods of each leg fused medially; not fused to exopod. Endopodal lobe reduced with 2 pinnate setae of very unequal length. Exopod with 5 pinnate setae, inner seta small, middle seta longest.

P6 a single plate fused to somite proximally (Fig. 11A), with 3 pinnate setae on each side (Fig. 11C).

REMARKS

(i) Synonymy

The Alaskan material on which the above redescription is based, was first described in detail in an excellent paper by

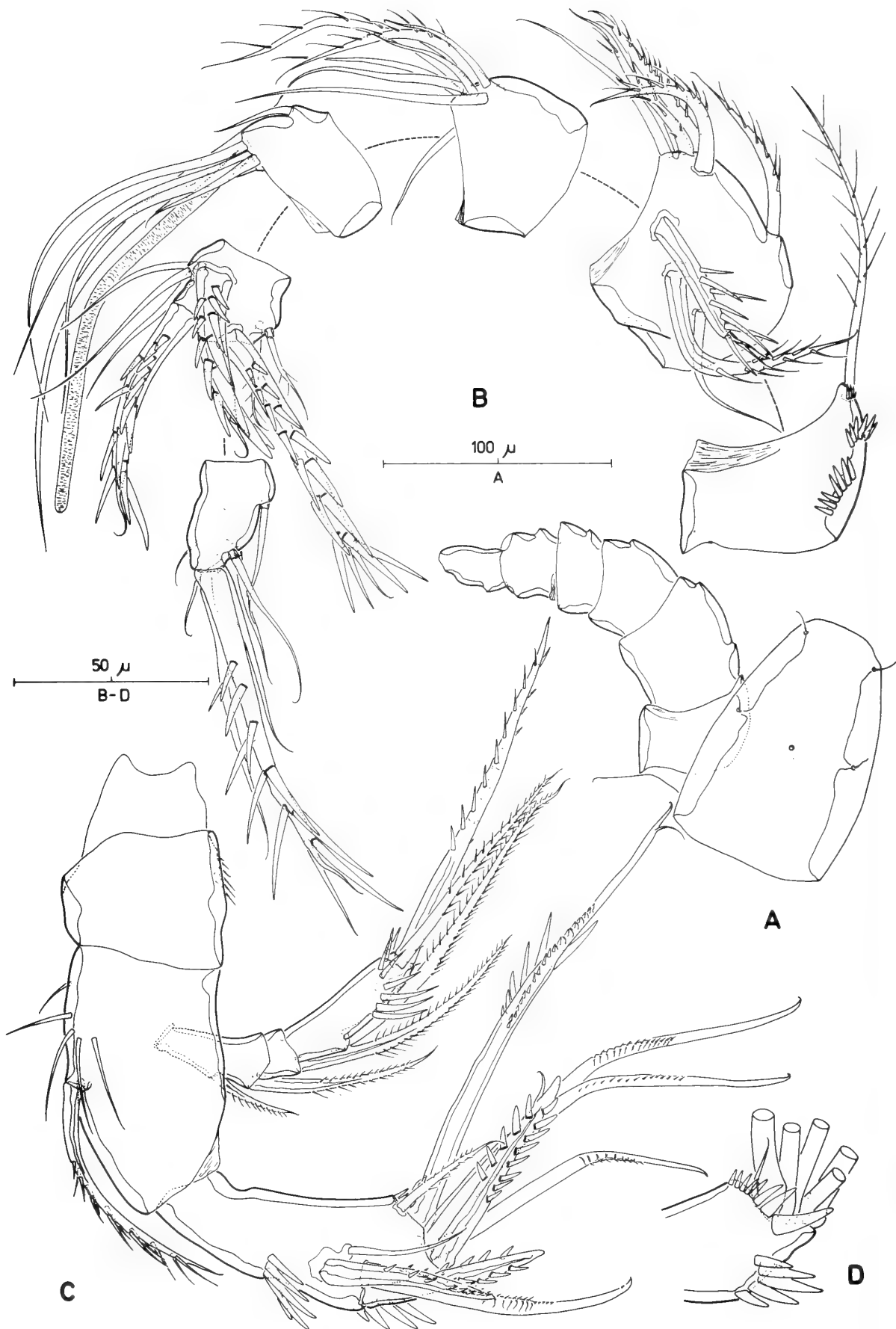


Fig. 2 *Archisenia sibirica* comb. nov. A, Rostrum and female antennule (armature omitted); B, female antennule (disarticulated); C, antenna, anterior view; D, antennary endopod, posterior view of distal margin.

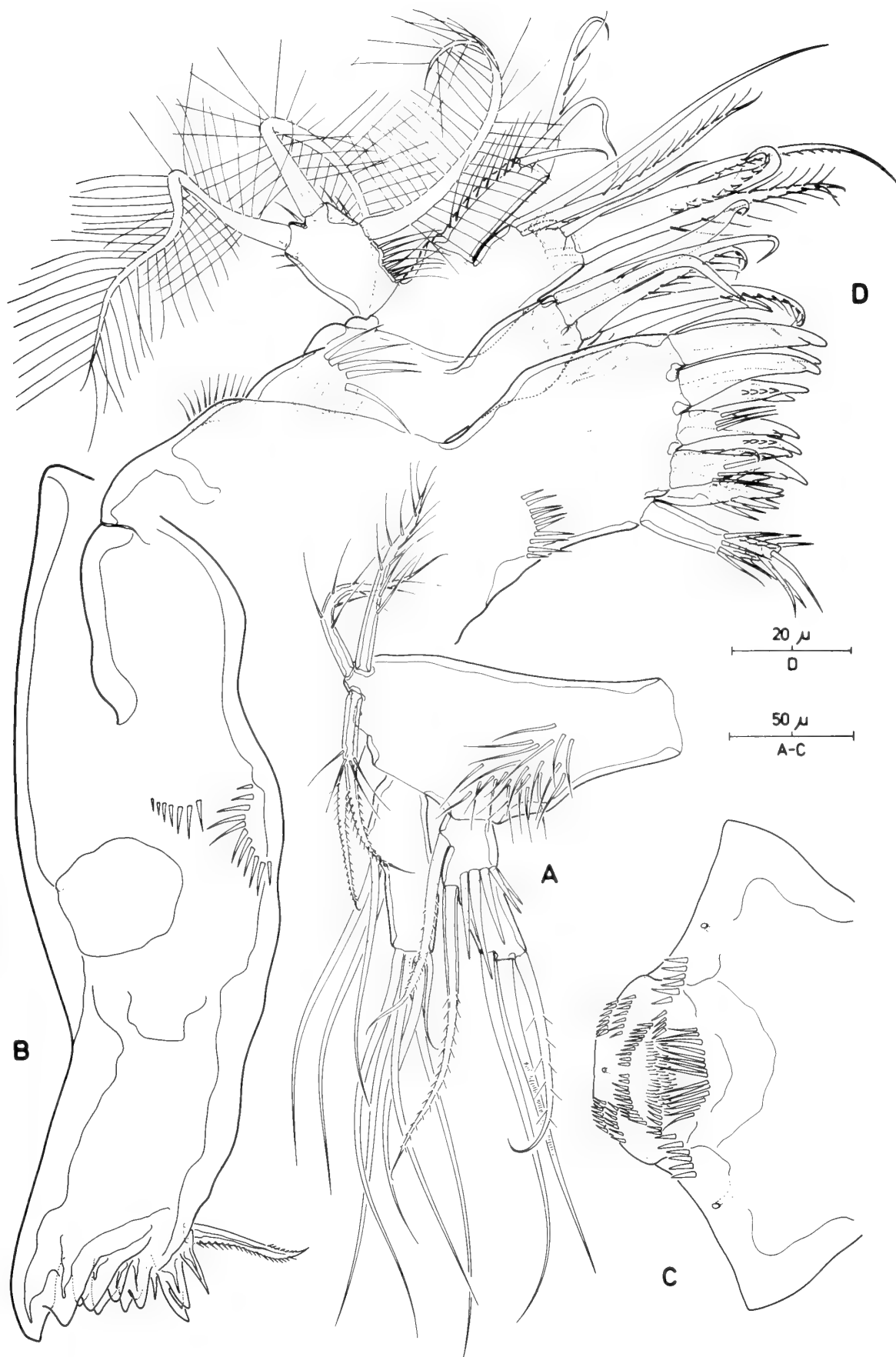


Fig. 3 *Archisenia sibirica* comb. nov. A, Mandibular palp; B, mandibular gnathobase; C, labrum; D, maxillule.

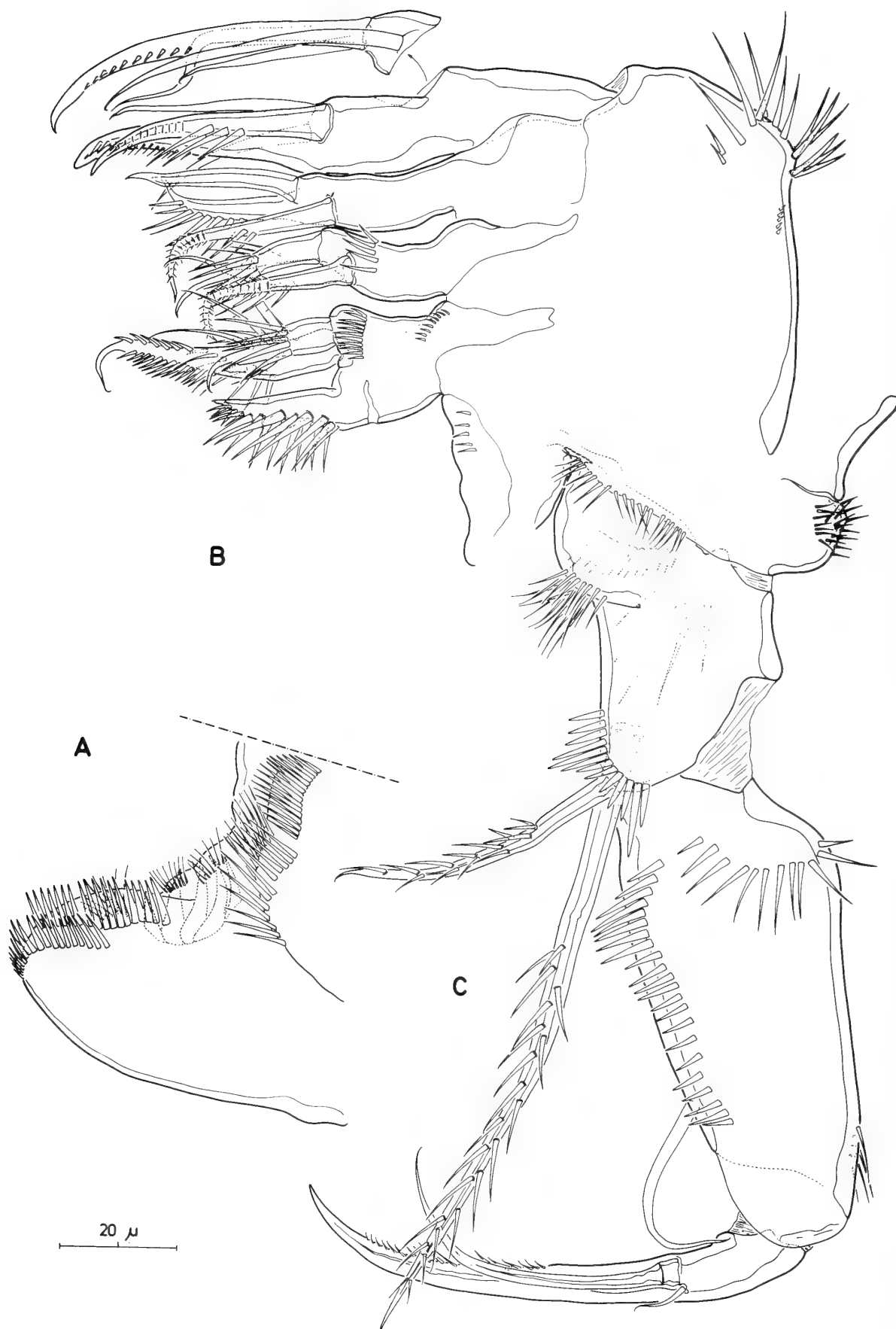


Fig. 4 *Archisenia sibirica* comb. nov. A, Right paragnath, posterior view; B, maxilla with disarticulated endopod; C, maxilliped.

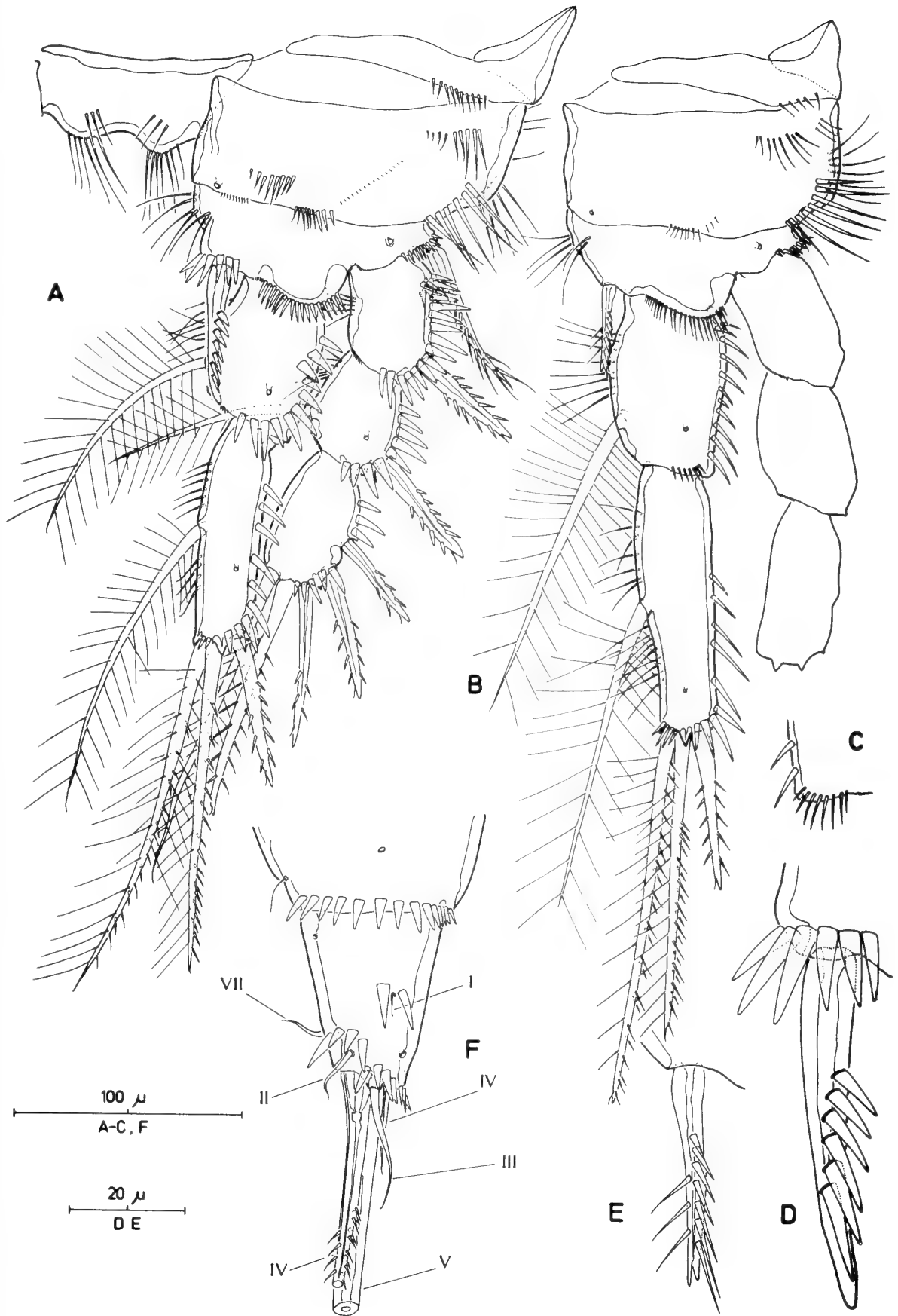


Fig. 5 *Archisenia sibirica* comb. nov. A, Female P1, anterior view; B, male P1, protopod and endopod, anterior view; C, male P1, distal margin of enp-1 of other side; D, female P1 inner basal spine; E, male P1 inner basal spine; F, caudal ramus, lateral view.

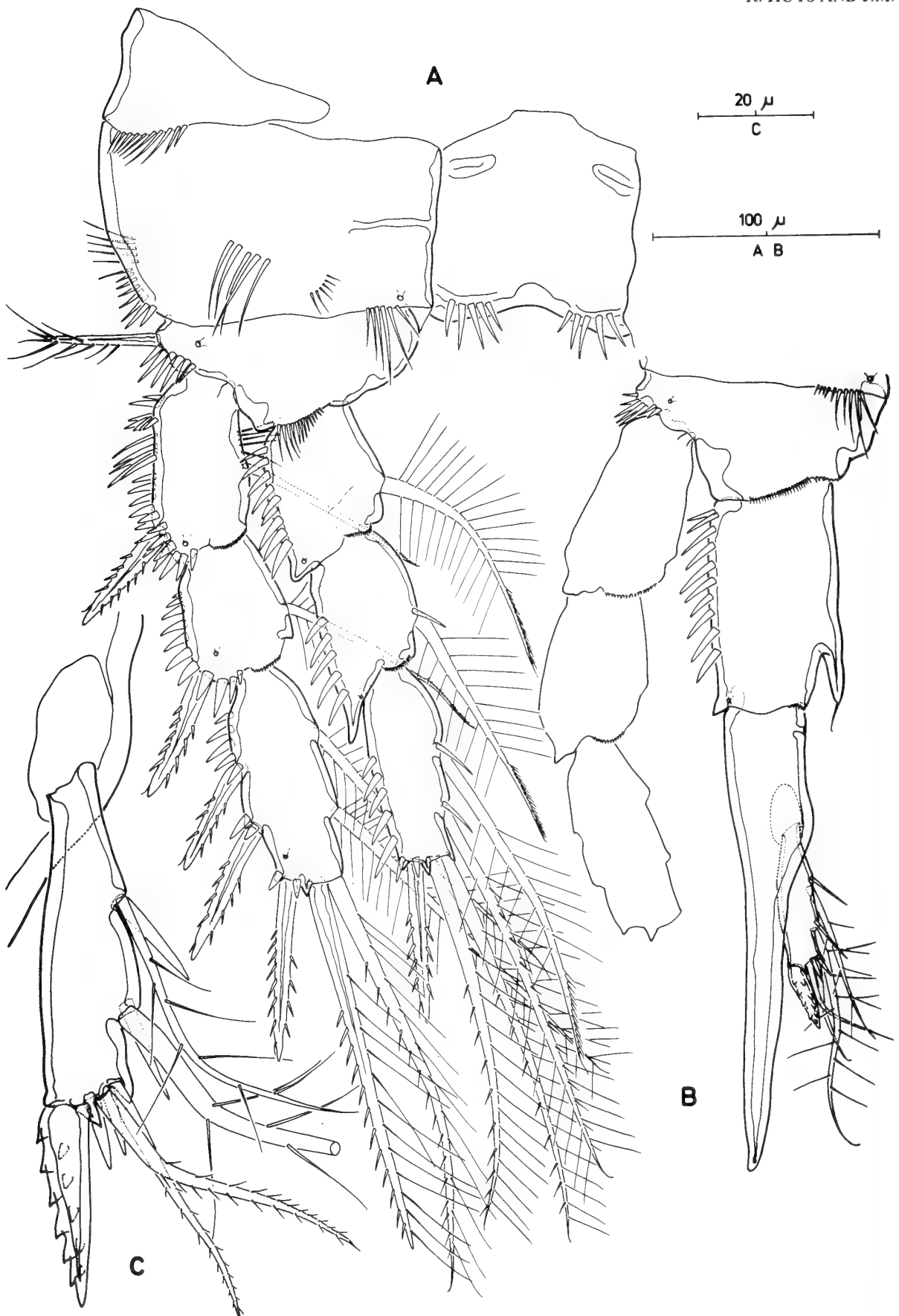


Fig. 6 *Archisenia sibirica* comb. nov. A, Female P2, anterior view; B, male P2 basis and endopod, anterior view; C, male P2 endopod distal segment, posterior view.

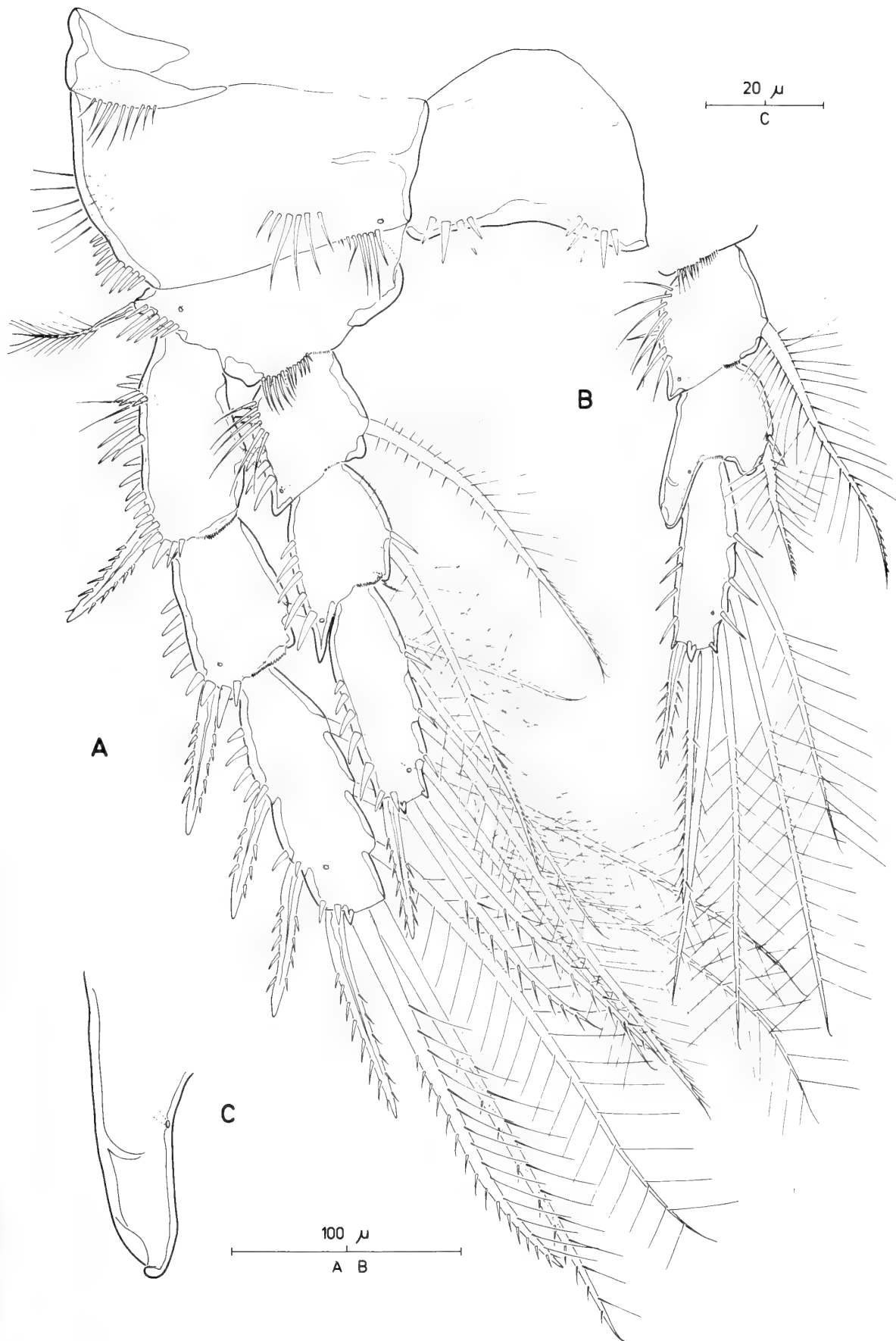


Fig. 7 *Archisenia sibirica* comb. nov. A, Female P3, anterior view; B, male P3 endopod, anterior view; C, male P3, detail of outer apophysis of enp-2.

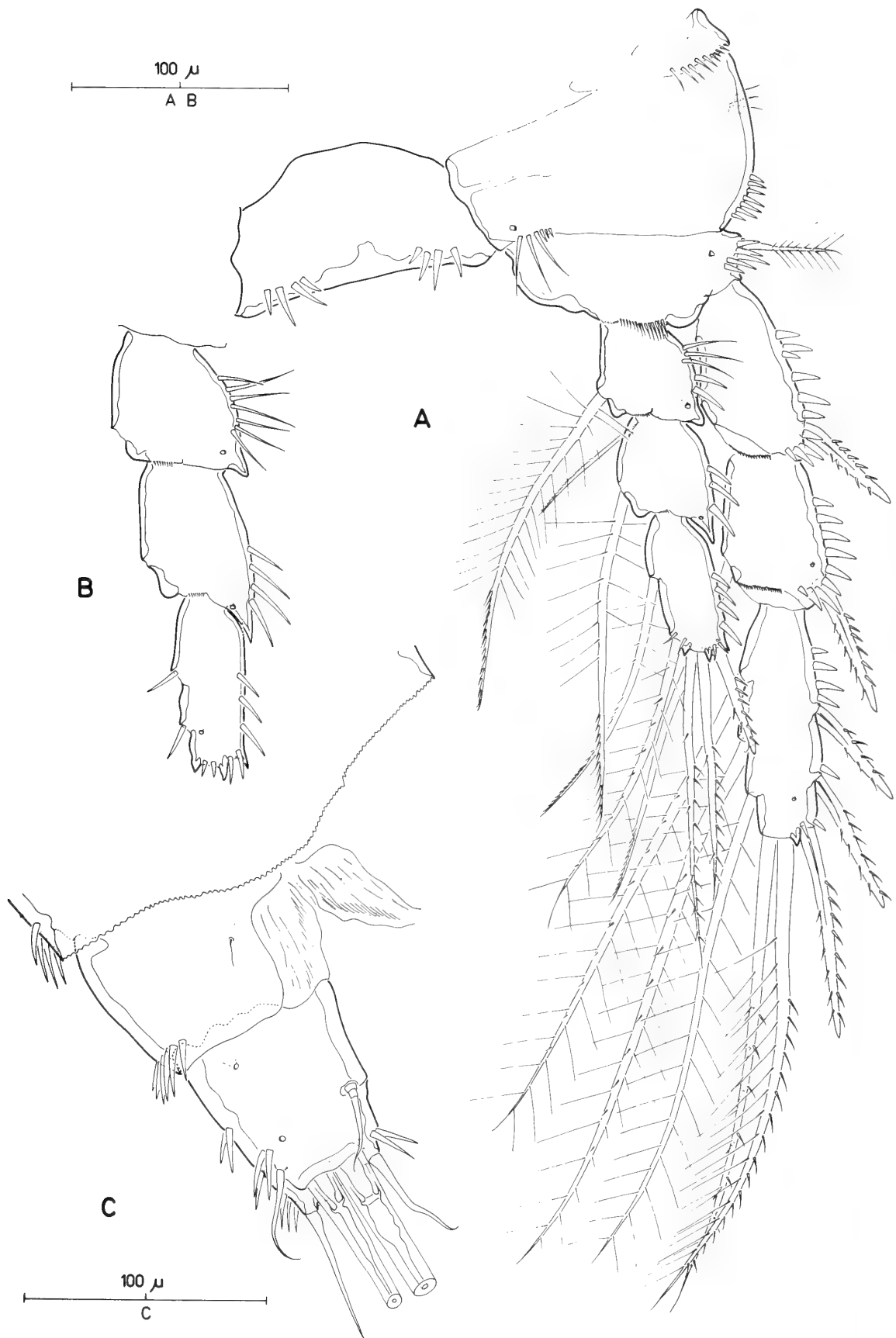


Fig. 8 *Archisenia sibirica* comb. nov. A, Female P4, anterior view; B, male P4, contours of endopod; C, pseudoperculum, anal somite and left caudal ramus in dorsal view.

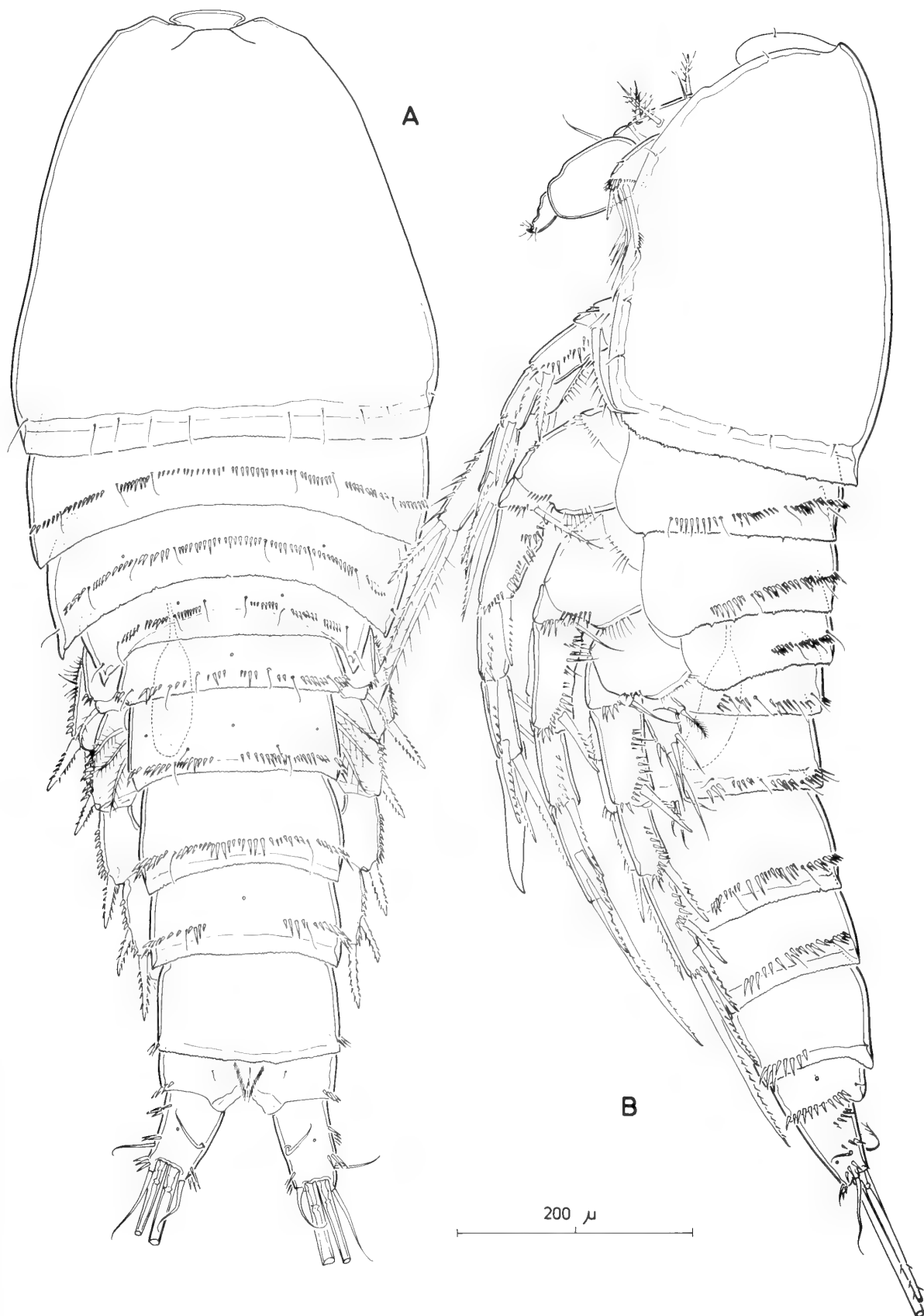


Fig. 9 *Archisenia sibirica* comb. nov. A, Male habitus, dorsal; B, same, lateral. [Sensillae on cephalothorax omitted.]

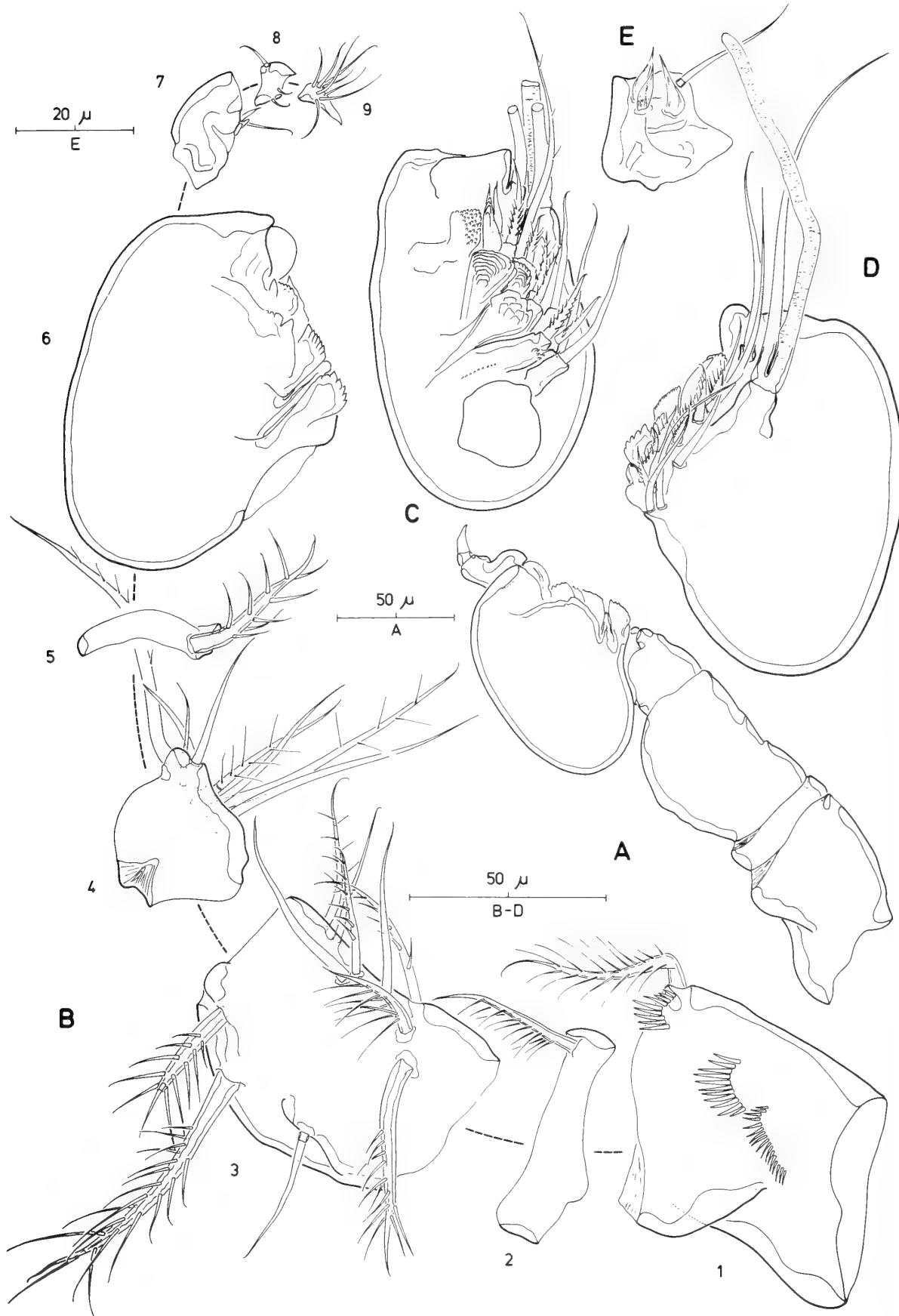


Fig. 10 *Archisenia sibirica* comb. nov. A, Male antennule (armature omitted); B, male antennule, disarticulated (armature of segment 6 omitted); C, male antennule segment 6, anterior view; D, same, ventral view; E, male antennule segment 7, anterior view.

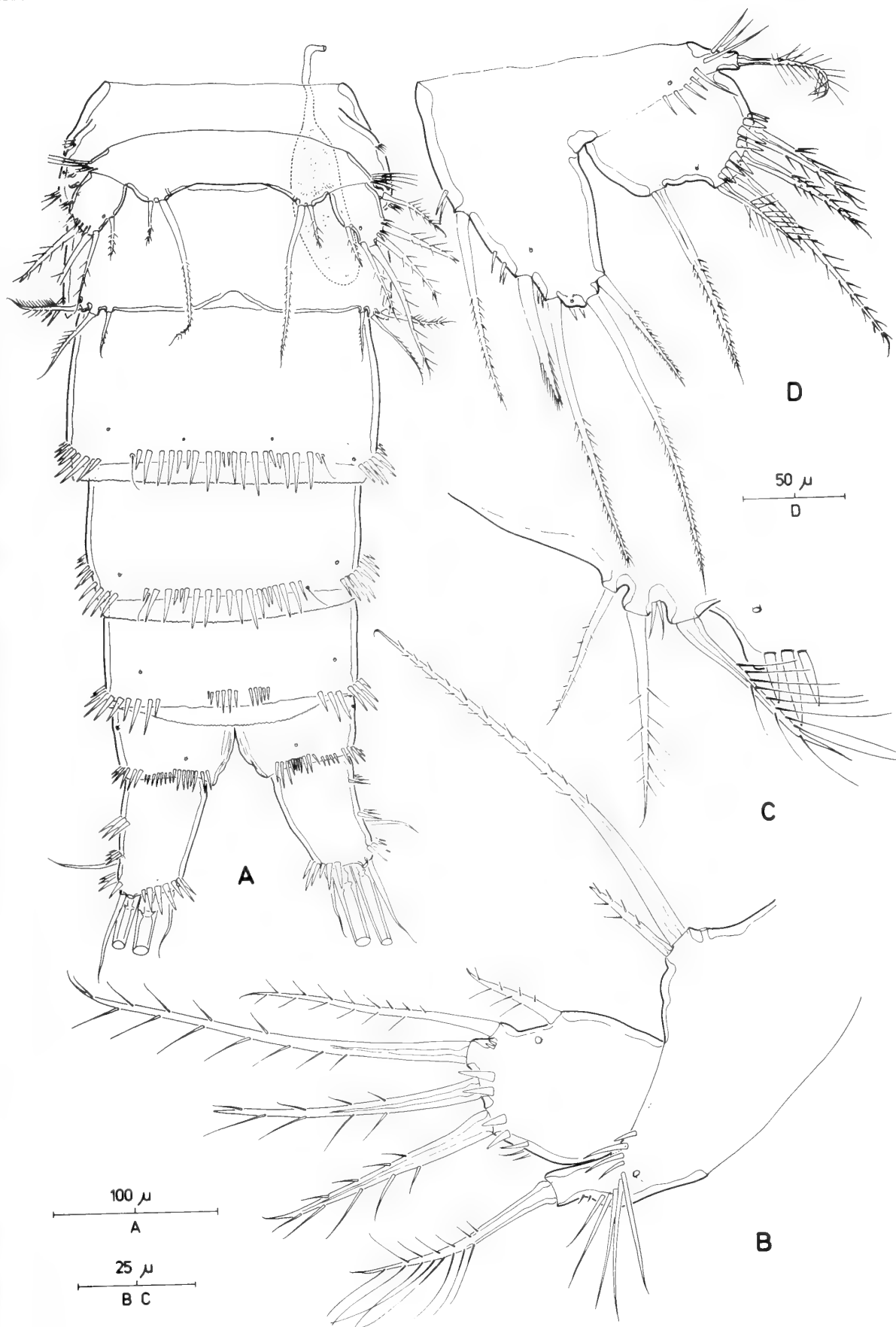


Fig. 11 *Archisenia sibirica* comb. nov. A, Male urosome, ventral view; B, male P5; C, male P6 armature; D, female P5.

Wilson (1966). There are slight discrepancies between these 2 descriptions which should be noted because of their possible phylogenetic significance. The rostrum does articulate with the cephalothorax and there are 2 accessory setae at the base of the maxillipedal claw. In the female there is no aesthetasc on the terminal segment of the antennule and the outer distal corner of enp-2 in P2 and P3 is significantly attenuated but that of enp-1 is normal (especially compared to the condition in *Psammis*). In the male the antennule is distinctly 9-segmented with segment 6 being swollen and bearing an aesthetasc; the distal outer element of P2 enp-3 is not completely fused to the segment but articulates along the anterior surface and partially articulates on the posterior surface; and there is no sexual dimorphism in P4 enp-2 (Fig. 8B).

We have been unable to locate the type, or any other, material of *D. sibirica* and therefore, like Wilson (1966), have had to rely on Sars' (1898) original description and figures. A study of these has led us to conclude that there are no real differences between *D. stefanssoni* and *D. sibirica*. We agree with Wilson's interpretation of the swimming leg setation. The original copy of Sars' paper in our possession also shows faint lines where the seta should be on P2-P4 exp-1 and in no other species in any paranannopid genus is this seta absent in the female when it is present in the male. Although Sars (1898) states in his text that the female antennule is 5-segmented, close scrutiny of his drawing (Plate X, Fig. 4) reveals that the terminal segment is at least partially divided into two segments and that the arrangement of the pectinate spines (3 on segment 5 and 1 at the apex of segment 6) is exactly the same as in *D. stefanssoni*. Further Sars has clearly misinterpreted the segmentation of the male antennule in that he has combined segments 1 and 2 as shown by the fact that his segment 1 bears 2 setae, a condition found in no other Paranannopidae. Wilson (1966) concluded that the only real difference between *D. stefanssoni* and *D. sibirica* was the absence in the latter of the distinctive outer distal spine on P2 enp-3 in the male. However, Sars' drawing of this limb (Plate X, Fig. 16) shows only 4 elements on enp-3 instead of 5, as in the female, and it is possible that the crucial one (the outer spine) is concealed behind the large apophysis on enp-2. This interpretation is supported by the fact that, irrespective of the degree of modification in males, the number of elements on P2 enp-3 is always the same in both sexes, except in the genera bearing claviform aesthetascs on the mouthparts (Gee & Huys, 1991) where the distal outer spine is further modified into a non-articulating apical apophysis.

These observations, coupled with such factors as similarity of size (they are the largest known members of the Paranannopidae except for *Psammis borealis* Klie, 1939 whose taxonomic position is unclear) and the peculiar identical distribution of setae on the distal margin of the female P5, lead us to the conclusion that the two species are synonymous and have a circum-polar distribution. Fig. 13 shows that the most easterly record of *D. sibirica* at Wrangell Island (Yashnov, 1935) is very close to the most westerly record of *D. stefanssoni* on the Chukchi Sea coast of Alaska (Wilson, 1966). The only record of the species outside the Arctic Circle is that of Wells (1965) from Loch Nevis on the west coast of Scotland and this must be regarded as doubtful (original specimens no longer available for re-examination). Further, both *D. stefanssoni* and *D. sibirica* have been recorded from estuaries and in brackish water, a most unusual habitat for members of this family. All other species are found only in

sublittoral marine habitats although *Danielssenia typica* Boeck, 1872, the other species with a known global distribution, has been recorded from the Baltic Sea (Veldre & Mäemets, 1956; Arlt, 1983), a region of lowered salinity.

(ii) Autapomorphies of *Archisenia*

Turning now to consider the taxonomic status of *D. sibirica*, its distinction from other members of the genus *Danielssenia* was suggested by Lang (1944) who divided *Danielssenia* into 2 groups, the *typica* group and the *sibirica* group. The latter he characterized by: (i) antenna exp-1 with 2 setae; (ii) P4 enp-3 with 2 inner setae; (iii) the male P2 enp-1 with the inner seta transformed into a non-articulating process; (iv) the male P3 enp-2 with an outer hooked apophysis. This last character is now known to occur in all species of Paranannopidae and might even be a diagnostic character for a wider group of families. The first two characters, although diagnostic of *D. sibirica* in combination, are the plesiomorphic condition in the family and are found in a number of other genera. *Paranannopus*, *Psammis*, *Micropsammis* Mielke, and *Bathypsammis* gen. nov. also retain 2 setae on exp-1 of the antenna (all other genera bear only 1 seta on this segment) and *Sentirenia* Huys & Gee (= *Jonesiella* Brady, see below) and the male of *Fladenia* retain 2 inner setae on P4 enp-3. However, the transformation of the inner seta into a non-articulating spine on P2 enp-1 in the male is unique to this genus, as are the following autapomorphies: (i) the outer extension on P3 enp-2 in both sexes; (ii) the sigmoid, heavily sclerotized female copulatory duct; (iii) the sexual dimorphism of the inner basal spine of the male P1. Another character of phylogenetic significance is the loss of the inner seta on the male P2 enp-2. This character is also found in *Afrosenia spinipes* (Wells, 1967) and is regarded here as a product of convergence. A further character which is unique but difficult to quantify is the arrangement of the setation on the exopod of P5, with the inner seta well separated from the remaining setae. It is on the basis of all these characters that we have removed *D. sibirica* to a new genus leaving the *typica* group as the only species group in the genus *Danielssenia*.

(iii) Intersexuality

The male from East Greenland (Fig. 12), collected by Jespersen, proved upon examination to be an aberrant intersexual specimen. It has the male body facies, including a 6-segmented urosome (Fig. 12A), a well developed testis and vas deferens (however, a spermatophore has not been observed), and the male form of the P5 and P6. The endopods of P2 and P3 are also modified but differ from the typical male condition by the retention of certain female features.

The antennules resemble the female condition in all aspects: they are 6-segmented, lack any trace of a geniculation mechanism and possess the female armature pattern. The P1 (Fig. 12B) basis and endopod show the same spinule arrangement as in the female but size and shape of certain spinule rows approach the male condition. The P2 endopods are not identical on both sides (Figs. 12C-D) and show a combination of male and female characteristics. The proximal segment and its basal pedestal are moderately enlarged but the spinule at the base resembles the female condition and the inner seta is — though being shorter than in the female — not transformed into a spinous process. The outer apophysis

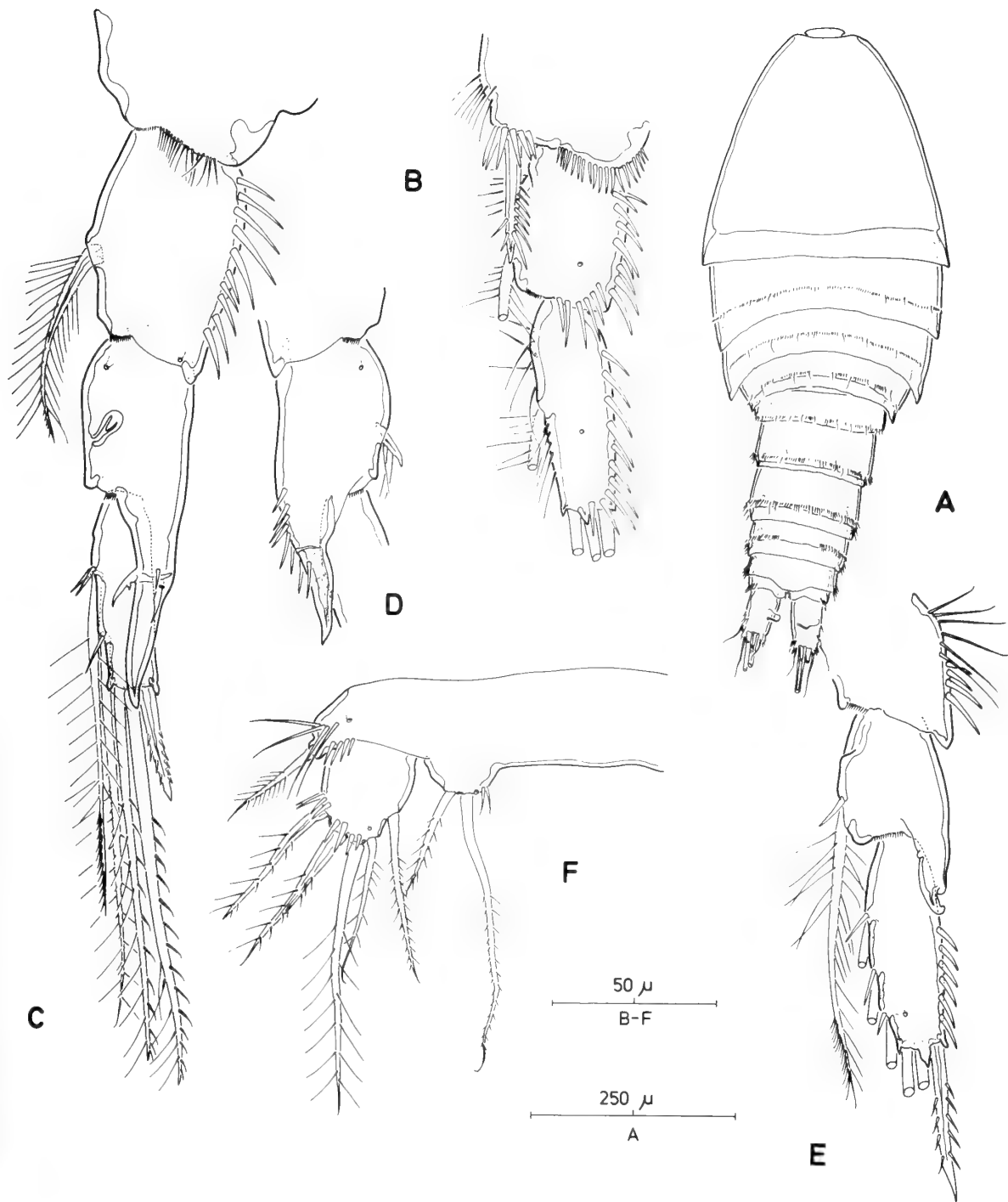


fig. 12 *Archisenia sibirica* comb. nov. Intersex specimen from Greenland. A, Habitus, dorsal view; B, P1, endopodal segments; C, P2, endopod of right side; D, P2, middle endopod segment of left side; E, P3 endopod; F, P5.

of the middle segment is distinctly shorter than in the typical male and its outer margin might bear spinules as in the female; the inner seta — completely missing in the male — is represented by a vestigial spine which is either entirely (Fig. 12C) or partly (Fig. 12D) invaginated. The distal segment is almost identical to the female condition. The P3 endopod is modified as in the male except that the inner seta of the middle segment is distinctly longer than in the typical male (but shorter than in the female). The P4 endopod grossly resembles the male condition. The P5 also has the basic male outline but the endopodal lobe is slightly more pronounced and the inner exopodal seta is distinctly longer.

Intersexuality within the Harpacticoida appears to be very rare. Klie (1944) describes a female specimen of *Amphiascoides debilis* (Giesbrecht, 1881) from Helgoland which displayed the male condition for the antennules (i.e. haplocer) and the first thoracopods (i.e. modified basis) and the female condition for the genital somite and the remaining appendages except for the P2 endopod which combined both male and female features. Recently, Moore & Stevenson (1991) found that 90% of a population of *Paramphiascella hyperborea* (T. Scott, 1903) in the vicinity of a sewage outfall in the Firth of Forth, Scotland, were intersex specimens. In the majority of these the prosome (including the antennules and swimming legs) exhibited the female condition whilst the urosome had the male condition of 6 distinct somites and a plate-like P6, although the P5 was more similar to that of the female. At the same site, a small number of intersex specimens of *Stenhelia gibba* Boeck, 1864 and *Halectinosoma similidistinctum* Lang, 1965 were also found. Intersexuality is more common in other orders of copepods, particularly the calanoids *Eudiaptomus vulgaris* (Schmeil, 1898), *Arctodiaptomus* (*Rhabdodiaptomus*) *alpinus* (Imhof, 1885), *Eudiaptomus gracilis* (Sars, 1863), *Pseudocalanus elongatus* (Boeck, 1864), *Calanus hyperboreus* Krøyer, 1838, *Paracalanus parvus* (Claus, 1863) (Bremer, 1914; Pirocchi, 1940; Cattley, 1949; François, 1949; Conover, 1965; Ianora *et al.*, 1987) and cyclopoids *Megacyclops gigas* (Claus, 1857) and *Megacyclops viridis* (Jurine, 1820) (Mrázek, 1913; Coker, 1938).

In natural populations the frequency of occurrence of intersexuality appears to be very low and may be a result of infrequent chromosomal aberrations during embryonic development. In cases of higher incidence, various causes of intersexuality have been postulated. Coker (1938) attributed it to low temperature during naupliar development; Cattley (1949) to parasitism of the developmental stages by the marine ectoparasitic dinoflagellate *Blastodinium contortum hyalinum* Chatton; and Moore & Stevenson (1991) argued that the very high incidence of intersexuality in the vicinity of a sewage outfall strongly implicated some form of chemical pollution as the causative factor.

Genus *Danielssenia* Boeck, 1872

Since the publication of Lang's (1948) monograph a number of new species have been assigned to the genus *Danielssenia* but recent analyses have shown this to be a heterogeneous assemblage. In previous papers (see also Table 1) we have removed *D. intermedia* Wells, 1965 to the genus *Fladenia*; *D. perezi* Monard, 1935 (syn. *D. paraperezi* Soyer, 1970) and *D. eastwardae* Coull, 1971 to the genus *Sentirenia* and propose to remove *D. spinipes* Wells, 1967 and *D. minuta* Coull, 1969 to two other new genera (Gee & Huys, 1990; Huys & Gee, 1992, in press). This has restricted the genus *Danielssenia* to

the following species: *D. typica*; *D. quadriseta* Gee, 1988; *D. reducta* Gee, 1988; *D. robusta* Sars, 1921 and *D. similis* Chislenko, 1971. The status of *D. fusiformis* (Brady, 1880), previously been synonymized with *D. typica* (cfr. Shen & Bai, 1956; Gee, 1988b) is reconsidered here.

(i) *Danielssenia fusiformis* (Brady, 1880) nec Sars (1910)

Brady (1880) created the genus *Jonesiella* to accommodate two new species, *J. fusiformis* (Brady & Robertson) and *J. spinulosa* (Brady & Robertson), and provided illustrated descriptions for these species. Brady remarked that both species had already been listed in an earlier report (Brady & Robertson, 1876) as *Zosime* (?) *fusiformis* and *Z. spinulosa*, respectively, and therefore unjustly concluded that both authors had to be credited with the authorship. This state of affairs has perpetuated in the nomenclature, even to the present (e.g. Gee, 1988b), though it is clear that Brady & Robertson's species names are mere *nomina nuda* and only Brady (1880) should be cited as the author of both *Jonesiella* species. Norman & Scott (1906) were the first to list *J. spinulosa* Brady, 1880 as a junior synonym of *Danielssenia typica* Boeck, 1872 and also changed *J. fusiformis* Brady, 1880 into *D. fusiformis*. Both species were redescribed and illustrated by Sars (1910) who admitted that they were very similar. It were also Sars' descriptions that led Shen & Bai (1956) to conclude that both species were identical, and after careful examination of Sars' material Gee (1988b) formally relegated *D. fusiformis sensu* Sars (1910) to a junior synonym of *D. typica*. There is, however, considerable evidence that what Sars (1910) considered to be *D. fusiformis* in Norway is clearly different from Brady's (1880) original material from the Scilly Islands. Brady's type material does no longer exist, but his illustrations (Plate XLVIII, Figs 1–13) of the female antennule, mandible, maxilliped, P1, the fifth legs in both sexes and the male endopod P2 leave no doubt that his species is identical with *D. perezi* Monard, 1935, originally described from Roscoff and later also recorded from the Scilly Islands (Wells, 1968) — the type locality of *J. fusiformis*. Huys & Gee (1992) recently synonymized *D. paraperezi* Soyer, 1970 with *D. perezi* and established a new genus *Sentirenia* to include the latter species and *D. eastwardae* Coull, 1971. *Sentirenia* Huys & Gee, 1992, therefore, has to be relegated to a junior synonym of *Jonesiella*, thus encompassing the type species *J. fusiformis* Brady, 1880 nec Sars (1910) (syn. nov.: *Danielssenia perezi* Monard, 1935; *D. paraperezi* Soyer, 1970) and *J. eastwardae* Coull, 1971 comb. nov.

Thompson's (1893) illustration of the female antennule suggests that his record of *J. fusiformis* from Liverpool Bay is correct. Re-examination of specimens (7 ♀♀ labelled *D. fusiformis*; Norman collection, reg. no. 1911.11.8.43561–565, gift from T. Scott; October 1899) collected in the Firth of Clyde indicates that the species might be distributed along the entire west coast of Britain. Lang's (1936a,b) specimens from the Öresund and Spitzbergen clearly belong to *D. typica*. All other records of *D. fusiformis* have to await confirmation (see list in Lang, 1948).

(ii) *Danielssenia robusta* Sars, 1921

Lang (1948) was of the opinion that *D. robusta* (and *D. perezi*) probably would require the definition of additional species groups inside the genus but as the males were still

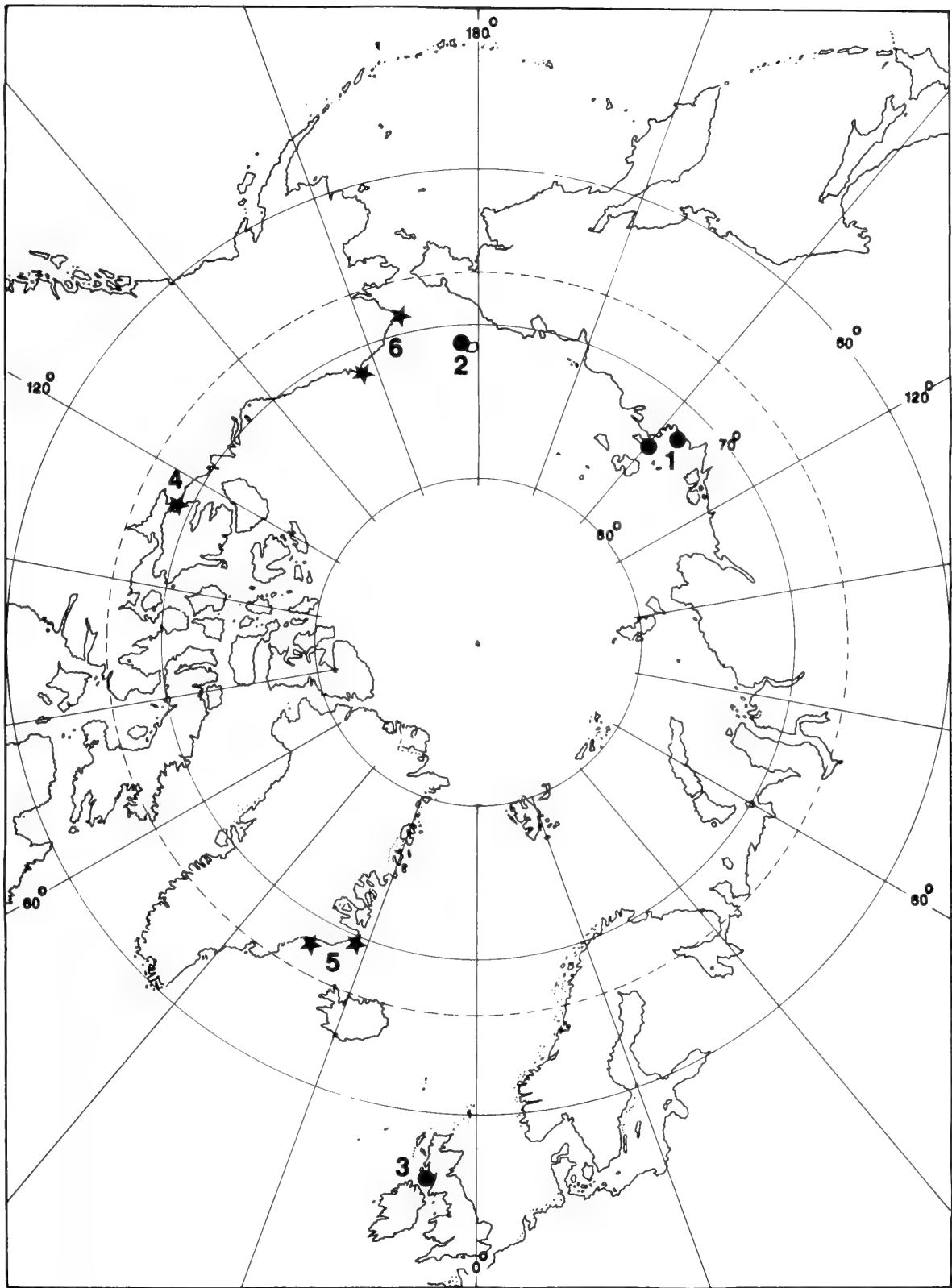


Fig. 13 Distribution map of *Danielssenia sibirica* (circles) and *D. stefanssoni* (stars). Records of 1. Sars (1898); 2. Yashnov (1935); 3. Wells (1965); 4. Willey (1920); 5. Jespersen (1939); 6. Wilson (1966). Arctic Circle shown by dashed line.

unknown at that time he regarded such an allocation as being premature. We have re-examined Sars' material of this species from Risør, Norway (13 ♀♀ and 1 copepodid V stage; Zoologisk Museum, Oslo, Reg. No. F20257) and found the following significant discrepancies from the original description of Sars (1921): (i) there is an inner seta on exp-1 of P2-P4; (ii) the inner element on enp-1 of P2-P4 is a pinnate spine; (iii) the P5 baseoendopod has 4 setae, the second inner one being much smaller than the others; (iv) the P5 exopod is fused to the baseoendopod on the posterior surface. Further, we have made a detailed comparison of these females with the recently discovered female of *D. intermedia* (which was assigned to the genus *Fladenia* by Gee & Huys (1990)) and have found them to be identical. Therefore *D. robusta* must be referred to the genus *Fladenia* whose type species now becomes *F. robusta* (Sars, 1921) comb. nov. as this has priority over *F. intermedia* (Wells, 1965). *F. robusta* has also been recorded from the Mediterranean by Por (1964), who found one female in 470 m off the coast of Israel, and Soyer (1970) who found 18 adult females at depths ranging from 50 to 420 m in the vicinity of Banyuls-sur-mer. Both authors state in their text that these specimens agree exactly with the original description. However, Por's (1964) Fig. 73 does show an inner seta on exp-1 of what is probably P4 (this limb is labelled P1 by Por but cannot possibly be so as the endopod is 3-segmented). This, taken in conjunction with his figure of the P5 (1964, Fig. 74) leaves little doubt that the Mediterranean material can be assigned to *F. robusta*, thus giving this species a Boreo-Mediterranean distribution similar to that of *Jonesiella fusiformis* (see Huys & Gee, 1992).

(iii) *Danielssenia similis* Chislenko, 1971

Chislenko (1971) distinguished *D. similis* from *D. typica* on the basis of the following characters: (i) Size, the specimen drawn in his Fig. 1 is approximately 0.9 mm long; (ii) a maxilliped with only 1 seta on the syncopa and a somewhat longer seta on the basis; (iii) the sexual dimorphism on P2 endopod, with the loss of the inner seta on enp-1 and of 1 seta on enp-3. The character of size is of no particular significance as it is within (but near the upper limit of) the size range of *D. typica* given by Gee (1988b). Similarly, the absence of a large seta on the basis of the maxilliped is of doubtful significance as this seta can be easily dislodged during dissection, as was the case in Sars' (1910) description of *D. typica* (see Gee, 1988b). The differences in sexual dimorphism of the male P2 endopod are more difficult to assess from drawings alone. However, it is highly improbable that the inner seta on P2 enp-1 is missing in the male when it is present in the female as this condition is found in no other member of this genus or indeed of the family as a whole. The same goes for a reduction in the number of setae on enp-3. In *Danielssenia*, the 2 terminal setae on this segment are very reduced and implanted close together and it is conceivable that Chislenko (1971) has combined these 2 fine setae and drawn them as one broad one. We believe that *D. similis* is referable to *D. typica* which has been shown to be the most variable species in the genus (Gee, 1988b) but without being able to examine topotype material we must regard it as a *species inquirenda*.

(iv) *Danielssenia typica* Boeck, 1872

The following material of the Norman collection (The Natural History Museum) has been examined (species name given

on the original museum label presented in parentheses):

1911.11.8.43451-470: vial containing > 400 specimens, mostly ♀♀, a gift from T. Scott; collected near Duke Buoy, Plymouth, 01 August 1889;

1911.11.8.43471-490: vial containing 23 ♀♀ and 1 ♂, a gift from T. Scott; collected from Varanger Fjord, East Finmark, Norway, 1890;

1911.11.8.43491-510: vial containing 31 ♀♀ and 3 ♂♂, a gift from T. Scott; collected from Vadsö, East Finmark, Norway, 03 July 1890;

1911.11.8.43511-530: vial containing 39 specimens (*D. typica*), a gift from T. Scott; collected in Trondhjem Fjord, Norway, 1893; 32 ♀♀ belong to *D. typica*, the other 7 ♀♀ belong to two different species of *Halectinosoma*;

1911.11.8.43531-540: vial containing 16 specimens (*D. typica*), a gift from T. Scott; collected from Inchkeith in Firth of Forth, October 1895. None of these specimens belongs to *D. typica*, instead the vial contained *Bradya* sp. (2 ♀♀, 8 copepodids), 2 ♂♂ *Robertsonia tenuis* (Brady & Robertson), 1 ♀ *Idomene coronata* (T. Scott) and 3 ♀♀ of a *Fladenia*-like paranannopid;

1911.11.8.43541-560: vial containing > 1000 specimens, mostly ♀♀, a gift from T. Scott; collected from Kames Bay, Isle of Cumbrae, 1888; a second lot of about 200 specimens from the same locality is registered under no. 1900.3.29.274;

1911.11.8.M.2299: 1 ♀ dissected on slide (*Jonesiella spinulosa*), dried out; collected in Trondhjem Fjord, Norway, 1893;

1911.11.8.M.2301: 43 specimens mounted *in toto* on slide (*Jonesiella spinulosa*), dried out; collected near Duke Buoy, Plymouth, 02 August 1889;

1911.11.8.M.2300: 8 specimens mounted *in toto* on slide (*Jonesiella spinulosa*), dried out; collected from Vadsö, East Finmark, Norway, 1890;

1900.3.6.644: 5 ♀♀ mounted *in toto* and 3 ♀♀ (one belonging to *Halectinosoma* sp.) dissected on slide (*Jonesiella spinulosa*); collected in Trondhjem Fjord, Norway, 1893.

Gee's (1988b) redescription of *D. typica* is updated here by the following observations and illustrations (Figs 14-16) based on specimens from Duke Buoy (closest to type locality):

Somatic hyaline frills of pedigerous and abdominal somites minutely dentate (Fig. 14A) except for the dorsal frill of P5-bearing somite which is deeply incised, forming rectangular lappets (Fig. 14A, B). Frill of cephalothorax smooth. Dorsal transverse spinule rows are found only on thoracic somites bearing P3-P5, the genital double-somite and second abdominal somite. Genital double-somite with continuous transverse chitinous rim dorsally, laterally and ventrally, marking original segmentation (Figs. 14A, D; 16D-E). Pseudopericulum (Figs. 14E-F) formed by deeply incised posterior extension of penultimate somite. Pattern of caudal rami setae as in Figs. 14E-F.

Rostrum (Fig. 16I) large, hyaline, with 2 pairs of minute sensillae; typically deflected (Figs. 14A-C).

Male antennule (Fig. 15G) 8-segmented or indistinctly 9-segmented; distal 2 segments very small and largely fused.

Mandible with blunt teeth and a single pinnate seta on gnathobase (Fig. 15A). Palp with short, equally long, 1-segmented rami (Fig. 15B); basis with row of very long setules proximally, inner margin with 1 short and 2 long setae; endopod with 2 lateral and 6 apical setae; exopod with

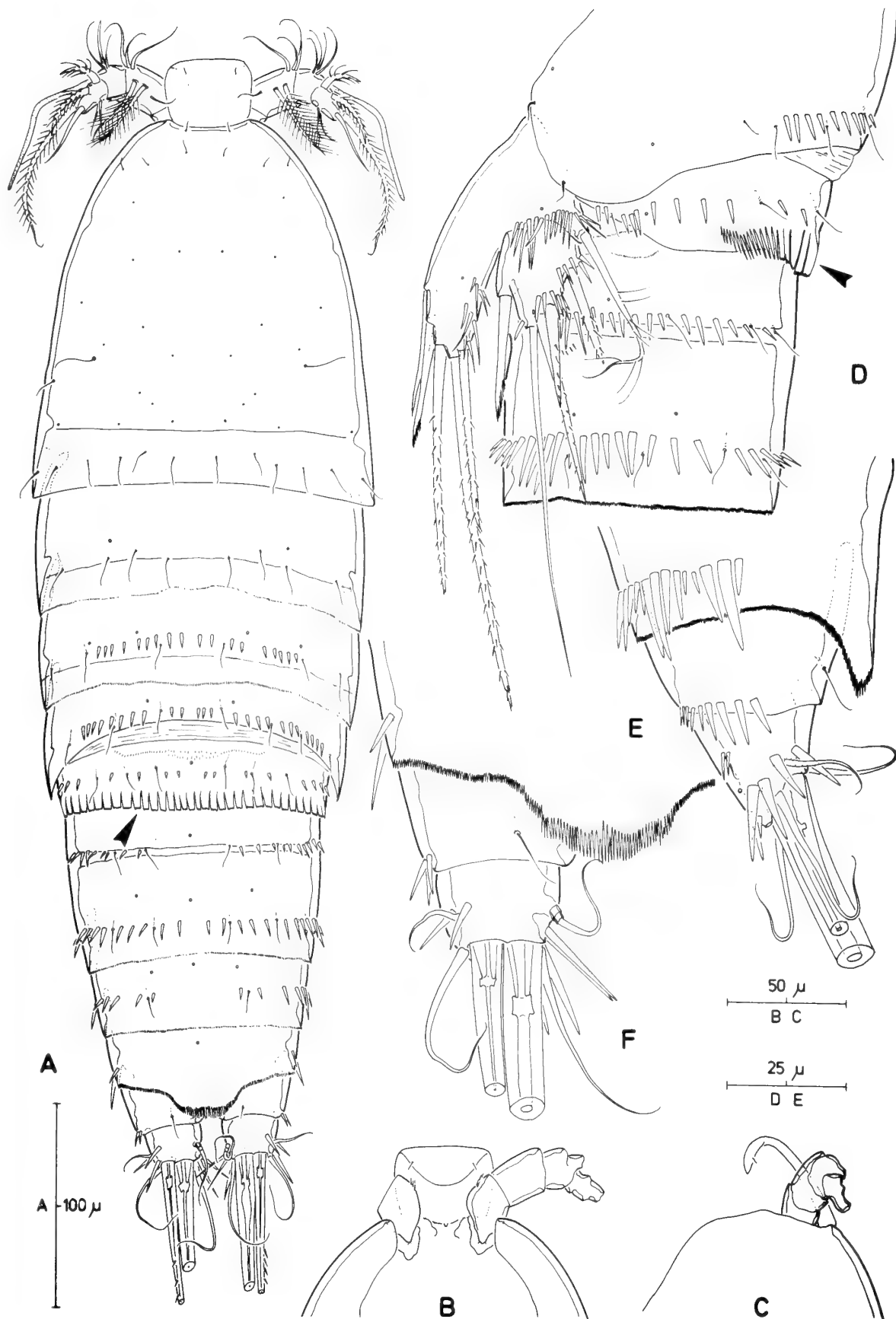


fig. 14 *Danielssenia typica*. Female: A, habitus, dorsal; B, rostrum and anterior part of cephalothorax, ventral; C, same, lateral; D, pleurotergite of P4-bearing somite, P5-bearing somite with fifth thoracopod and genital double-somite, lateral; E, pseudopericulum, anal somite and left caudal ramus, lateral; F, same, dorsal. [Incised hyaline frill of P5-bearing somite arrowed in A and D.]

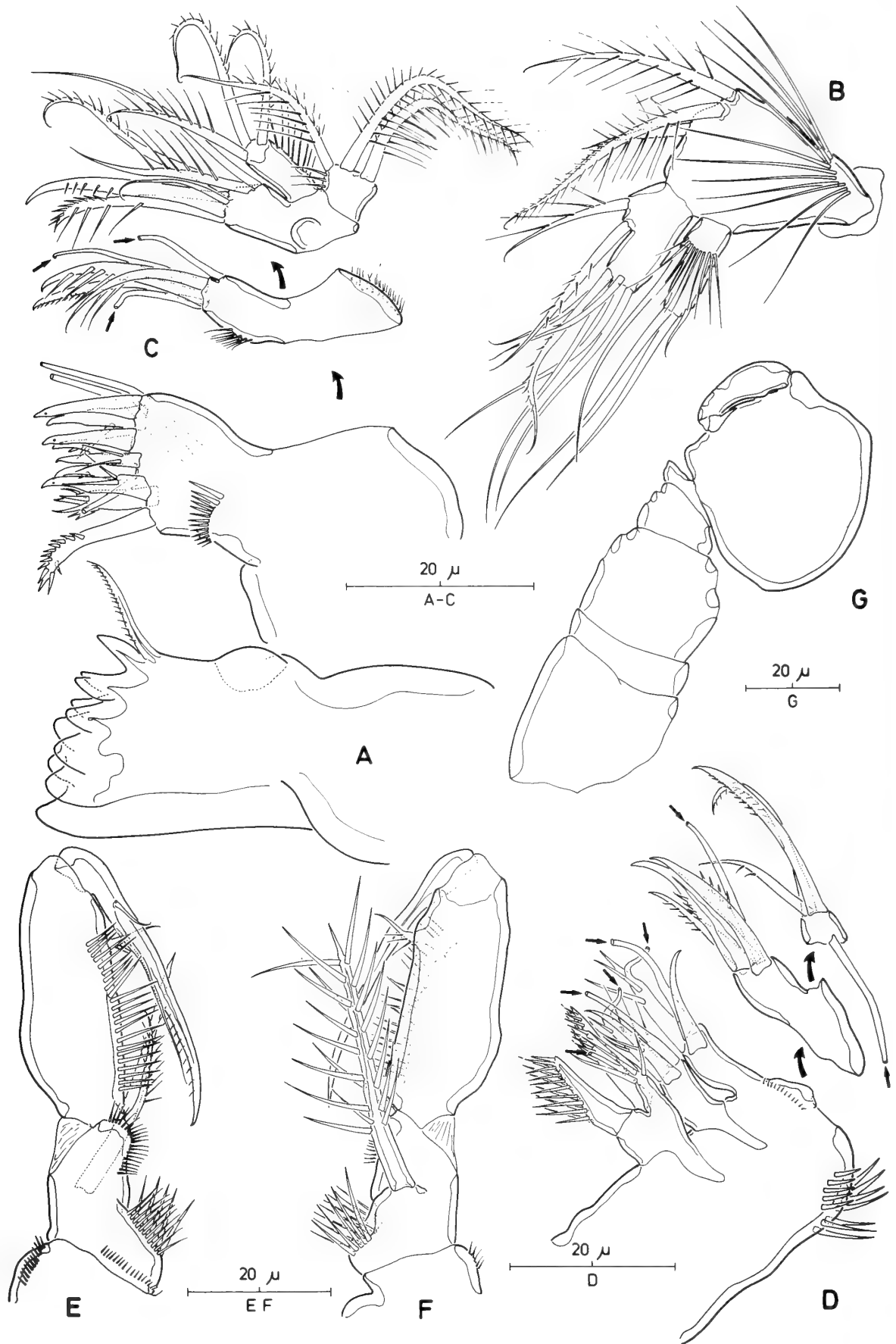


Fig. 15 *Danielssenia typica*. A, Mandible, gnathobase; B, mandible, palp; C, maxillula, posterior, showing disarticulated praecoxa, coxa and palp; D, maxilla, showing disarticulated syncoxa, basis and endopod; E, maxilliped, anterior; F, maxilliped, posterior; G, male antennule (armature omitted). [Tubular setae arrowed in C-D.]

row of long setules at 1/3 distance from the proximal margin, and 1 lateral, 1 subapical and 2 apical setae.

Maxillule (Fig. 15C). Praecoxal arthrite with 9 spines and 1 tubular seta around the distal margin, and 2 geniculate tubular setae on the anterior surface; coxal endite with 1 pinnate spine, 1 setulose claw, 1 smooth setae and 3 tubular setae; basal endites closely set, proximal with 2 setae, distal with 2 setae and 2 spines; rami with 3 setae each.

Maxilla (Fig. 15D). Praecoxal endite with 2 unilaterally pinnate spines and 1 basally fused spine bearing tubular extension. Coxal endites with 1 spine and 2 tubular setae each. Allobasis with 2 articulating claws, 1 pinnate spine and 1 tubular seta. Endopod with 1 tubular seta, 1 spine and 2 pinnate setae.

Maxilliped (Figs 15E–F). Syncoxa with 1 large setulose spine posteriorly and 1 smaller pinnate seta anteriorly. Basis with anterior row of long spinules and small, pinnate seta on palmar margin. Endopodal claw with 2 accessory setae.

Intercoxal sclerites of P2–P4 (Fig. 16H) not U-shaped and provided with large spinules on anterior surface (as in *Archis-enia*).

P2 endopod of male (Figs 16A–B). Inner setae of proximal and middle segments reduced compared to the female. Outer apophysis of middle segment very large, reaching far beyond the distal segment. Inner setae of distal segment spiniform and stouter than in the female; inner terminal seta reduced, with spatulate tip; outer terminal seta represented by small setule; outer spine curved at tip and standing on cylindrical process.

P3 endopod of male (Fig. 16C) with acutely recurved process anteriorly at outer distal corner of middle segment.

Genital field with minute copulatory pore (Fig. 16D) leading via short sclerotized duct to multi-chambered seminal receptacle (Figs 16F–G). Copulatory duct entering unpaired ventral chamber leading dorsally to paired reservoirs both anteriorly and posteriorly. Anterior reservoirs largest and extending to posterior part of P5-bearing somite (Fig. 16D). P6 in female represented by 1 plumose seta and 2 minute spiniform elements (Fig. 16E). P6 of male with 1 plumose and 1 pinnate seta (Fig. 16J).

REMARK. Shen & Bai (1956) pointed out that either 1 or 2 setae can be found on the middle endopod segment of P2, however, their figured specimen with 2 setae on this segment (Plate XI, Fig. 86) is almost certainly an aberrant case. The same applies to the armature of the baseoendopod of the male specimens reported on by Gee (1988b) where a ‘variable’ number of setae can be found; all setation patterns diverging from the typical bisetose condition are aberrations caused by abnormal copepodid development.

(v) Amended diagnosis

As a result of the arguments put forward above, the genus *Danielssenia* now contains only 3 well defined species and we have re-diagnosed the genus accordingly:

Paranannopidae. Body variable in size, slightly fusiform and dorso-ventrally flattened. Rostrum hyaline, large, typically deflexed, with 2 pairs of small sensillae. Somatic hyaline frills minutely dentate except for deeply incised frill on dorsal margin of P5-bearing somite. Original segmentation of female genital-double somite marked by complete subcuticular ridge; genital field with small copulatory pore; short copulatory duct leading to seminal receptacle with paired,

anteriorly directed chambers extending to anterior margin of genital double-somite; P6 with 1 outer plumose seta and 2 minute spiniform elements. Pseudopericulum hyaline with deeply incised margin. Caudal rami parallel, broader than long, seta I minute. Female antennule 4-segmented; aesthetasc on segment 3; terminal segment with strong pinnate spines. Antennary exopod 3-segmented with armature formula [1-1-3]. Mandibular coxa with blunt teeth and 1 seta on gnathobase, basis broad with 3 setae on distal margin; endopod 1-segmented; exopod 1-segmented, with 1 lateral and 3 distal setae. Maxillule with 3 tubular setae, 1 pinnate seta and 1 spine on coxal endite; basal endite with 4 setae and 1 spine. Maxilla with tubular setae on coxal endites, allobasis and endopod; praecoxal endite with 3 pinnate spines. Maxilliped subchelate with 1 large and 1 small seta on syncoxa; basis with small pinnate seta on palmar margin, endopodal claw with 2 accessory setae. P1 exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod 2-segmented, enp-2 4 times longer than broad, inner seta implanted medially. P2–P4 intercoxal sclerites with spinules on distal margin; rami 3-segmented; exp-1 without inner seta. Armature formula of P1–P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	0.1.(1–2)23	1.1.221
P3	0.1.(1–2)23	1.1.(1–2)21
P4	0.1.(2–3)23	1.1.(0–1)21

Female fifth pair of legs not fused medially; exopod and baseoendopod separate, each with 4 or 5 setae.

Male with sexual dimorphism on antennule, P2 endopod, P3 endopod, P5, P6, and in genital segmentation. Antennule 8- to 9-segmented, subchirocer; segment 6 very swollen, with aesthetasc. P2 enp-2 with inner seta, outer distal corner attenuated into a long apophysis reaching far beyond the distal border of enp-3; enp-3 with distal outer spine and 2 terminal setae very reduced, inner setae spiniform and larger than in female. P3 enp-2 with outer distal corner attenuated into a recurved apophysis. P5 of each side fused medially; baseoendopod and exopod separate with 2 and 4 or 5 setae, respectively. P6 symmetrical, fused to somite, with 2 setae each.

TYPE SPECIES. *D. typica* Boeck, 1872 (by monotypy). [syn.: *D. fusiformis* (Brady, 1880) sensu Sars (1910)].

OTHER SPECIES. *D. quadriseta* Gee, 1988; *D. reducta* Gee, 1988.

SPECIES INQUIRENDA. *D. similis* Chislenko, 1971.

Key to species

1. P2–P3 exp-3 with 2 inner setae, P4 enp-3 with 1 inner seta ... 2.
P2–P3 exp-3 with 1 inner seta, P4 enp-3 without inner seta
..... *D. reducta* Gee, 1988.
2. P3 enp-3 with 2 inner setae, P5 exopod with 5 setae in both sexes
..... *D. typica* Boeck, 1872.
P3 enp-3 with 1 inner seta, P5 exopod with 4 setae in both
sexes *D. quadriseta* Gee, 1988.

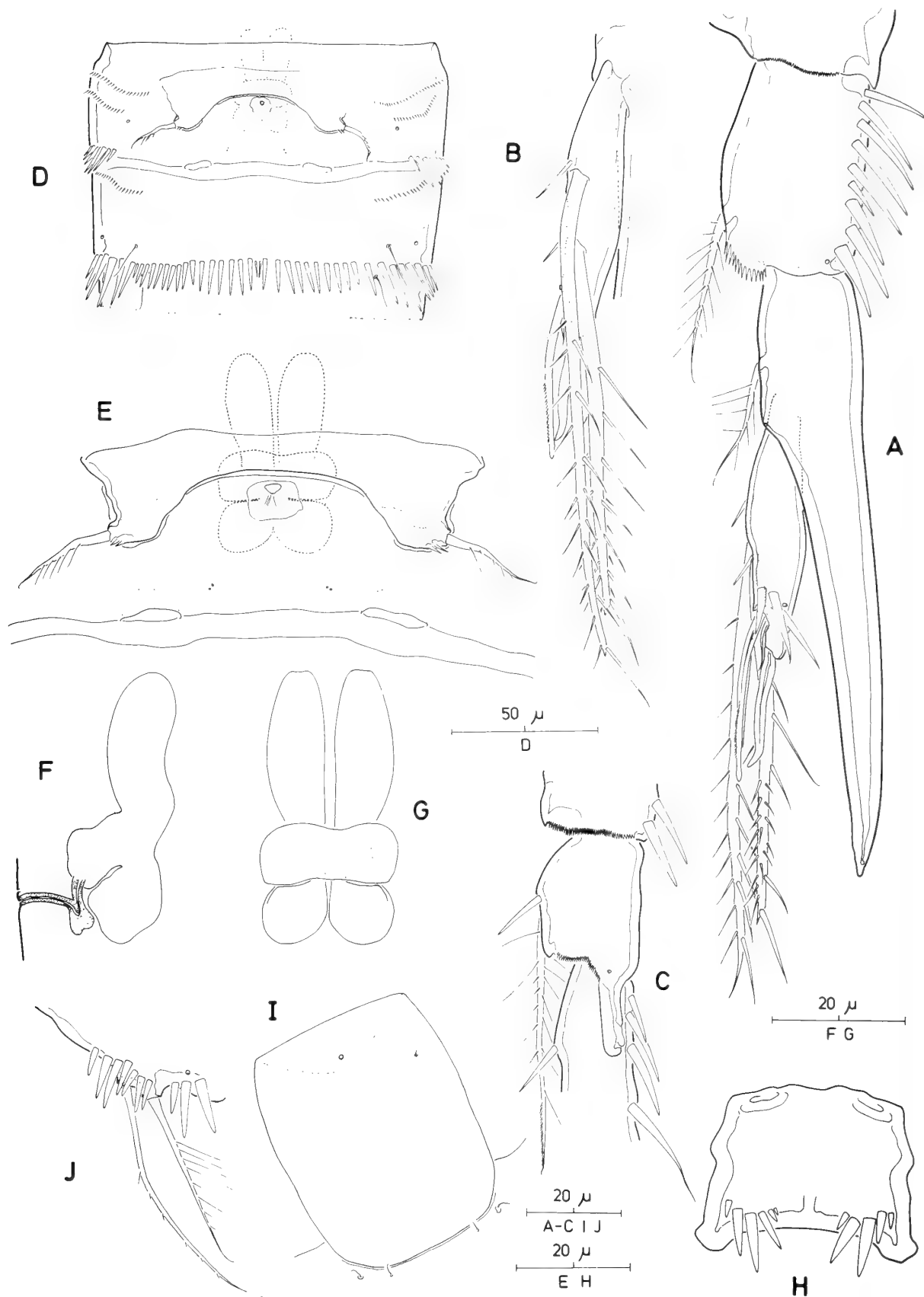


Fig. 16 *Danielssenia typica*. Male: A, P2 endopod, anterior; B, distal segment of P2 endopod, posterior; C, P3 endopod, middle segment, anterior; H, intercoxal sclerite P3; J, sixth leg. Female: D, genital double-somite, ventral; E, genital slit and copulatory pore; F, seminal receptacle, lateral; G, same, ventral; I, rostrum.

Genus *Bathypsammis* gen. nov.

SYNONYMY. *Psammis* Sars, 1910 (part.).

DIAGNOSIS. Paranannopidae. Body large, more or less cylindrical. Rostrum not hyaline, with 2 pairs of sensillae, anterior pair large. Somatic hyaline frills minutely dentate. Female genital double-somite with lateral and ventral sub-cuticular ridge, marking original segmentation; copulatory pore minute; copulatory duct and seminal receptacle unconfirmed; P6 with 2 setae and 1 setule in between. Pseudoperculum hyaline, vestigial. Caudal rami divergent, elongate (length about 5 times proximal width); with tuft of long setules near inner distal corner; dorsal surface with chitinated rim in anterior half. Female antennule 4-segmented; aesthetasc on segment 3; distal 2 segments with heavily pectinate spines. Antennary exopod 3-segmented with armature formula [2-1-3]. Mandibular coxa elongate, gnathobase with blunt teeth and spinule row; basis broad with 4 setae on distal margin; endopod 1-segmented, slightly longer than exopod; exopod 1-segmented with 1 lateral and 2 apical setae. Maxillule without modified spines on coxal endite; basal endite with 5 setae. Maxilla without tubular setae; praecoxal endite with 3 pinnate spines (1 fused to endite). Maxilliped subchelate; armature of syncoxa unconfirmed; basis with naked seta on palmar margin, endopodal claw with 2 accessory setae. P1 with very long outer basal seta reaching to middle of exp-3; exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod shorter than exopod; 2-segmented, enp-2 as long as enp-1, inner seta implanted at 1/3 distance from proximal margin. P2-P4 intercoxal sclerites with few long setules; rami 3-segmented; exp-1 with inner seta; female P2-P3 enp-2 without apophysis at outer distal corner. Armature formula of P1-P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.2.121
P3	1.1.323	1.1.121
P4	1.1.323	1.1.121

Female fifth pair of legs not fused medially; exopod and baseendopod fused to form a bilobate plate; exopodal lobe with 2 spines and 2 setae; endopodal lobe with 2 setae and 3 spines, the outer 2 of which are stubby.

Male unknown.

TYPE SPECIES. *Bathypsammis longifurca* (Bodin, 1968) comb. nov.

OTHER SPECIES. None.

ETYMOLOGY. The generic name is derived from the Greek *bathys*, meaning deep, and *Psammis*, probably the most closely related genus known in the Paranannopidae. Gender: feminine.

Bathypsammis longifurca (Bodin, 1968) comb. nov.

SYNONYMY. *Psammis longifurca* Bodin, 1968.

MATERIAL EXAMINED. From Dr Ph. Bodin: holotype dissected on 3 slides and now deposited in the collections of The Natural History Museum under reg. no. 1992.1091; Bay of

Biscay, Stn 308 (46°07' N; 05°00' W), depth 3950 m; coll. August 13 1963, R/V *Job-ha-Zelian*.

Bodin's (1968) excellent original description is supplemented here by the following observations and Figures 17-18.

Antennule 4-segmented, third segment homologous to segments 3-4 in *Archisenia*. Distal segment with large, swollen seta anteriorly near proximal corner; as pointed out by Bodin this segment is seemingly subdivided by the raised insertion site of one of the large pectinate spines (Fig. 18A). Armature formula: [1, 8, 14+ae, 16].

Mandibular gnathobase (Fig. 17B-C) with 4 long teeth, one trifold, slender element and 1 pinnate seta; a comb of spinules is present at the base of the smaller teeth. The endopod has 1 outer, 1 subapical and 6 apical setae (2 of which are fused basally).

Maxillule (Fig. 17D). Praecoxal arthrite with 9 spines and 1 tubular seta around the inner margin, and 2 geniculate tubular setae on the anterior surface; coxal endite with 4 setae, pinnate spine and straight spine with defined flexure zone and small pore near the apex; basal endite with 5 setae.

Maxilla (Fig. 18B-C) with praecoxal endite drawn out into heavily pectinate spine and bearing 2 articulating elements; coxal endites with 1 serrate spine and 2 setae each. Allobasis with 1 short and 2 long setae; endopod with 4 setae.

Maxilliped (Fig. 18D). Syncoxa missing in preparation. Basis with naked seta on inner margin, 2 spinular rows on anterior surface and another one on posterior surface; endopodal claw with 2 accessory setae.

Intercoxal sclerites of P2-P4 U-shaped (as in *Fladenia*) and provided with few long setules near lateral margins.

Fifth leg (Fig. 17E) with 2 large tube pores on anterior surface.

Genital field (Fig. 18E) with minute copulatory pore. The internal structures of the genital double-somite were destroyed during the dissection, so no observations of the copulatory duct and the seminal receptacles could be made.

Pseudoperculum very weakly developed. Distribution of caudal rami setae as in Fig. 18F-G; seta III dislodged in both rami, insertion site indicated by small socle (Fig. 18G).

P. longifurca does have certain features in common with *P. longisetosa* and *P. longipes*, namely: anterior pair of rostral sensillae enlarged (Fig. 17A); only 1 lateral seta on both rami of the mandible (Fig. 17B); 2 setae on exp-1 of the antenna; 2 setae on enp-2 of the P2; and fused rami in the female P5. However, *P. longifurca* lacks certain important features shared by the other two species, namely: no large strongly pinnate seta on the basis of the maxilliped, the seta on this segment being small and naked (Fig. 18D); the endopod of P2 is not distinctly longer than the exopod; the proximal inner seta of P2 enp-2 is not displaced to the posterior surface; the inner distal seta of P3-P4 enp-3 is not reduced; and, there is no attenuation of the outer distal corner of P2 enp-1. Finally, *P. longifurca* has a number of characters which are not shared by the other members of this genus such as: (i) a plume of long fine setules at the inner distal corner of the caudal ramus; (ii) an outer basal seta on P1 which is nearly as long as the exopod; (iii) a P1 endopod which is shorter than the exopod and in which both segments are equal in length; (iv) a P5 with peculiar spines on the endopodal lobe and a minute outer basal seta; (v) a primitive setal formula for the exopods of the swimming legs which is shared only by *Archisenia* and *Jonesiella*. On the basis of these characters we assign *P.*



Fig. 17 *Bathypsammis longifurca* comb. nov. Female: A, rostrum; B, mandible; C, mandible, gnathobase; D, maxillule, praecoxa disarticulated; E, P5, anterior.

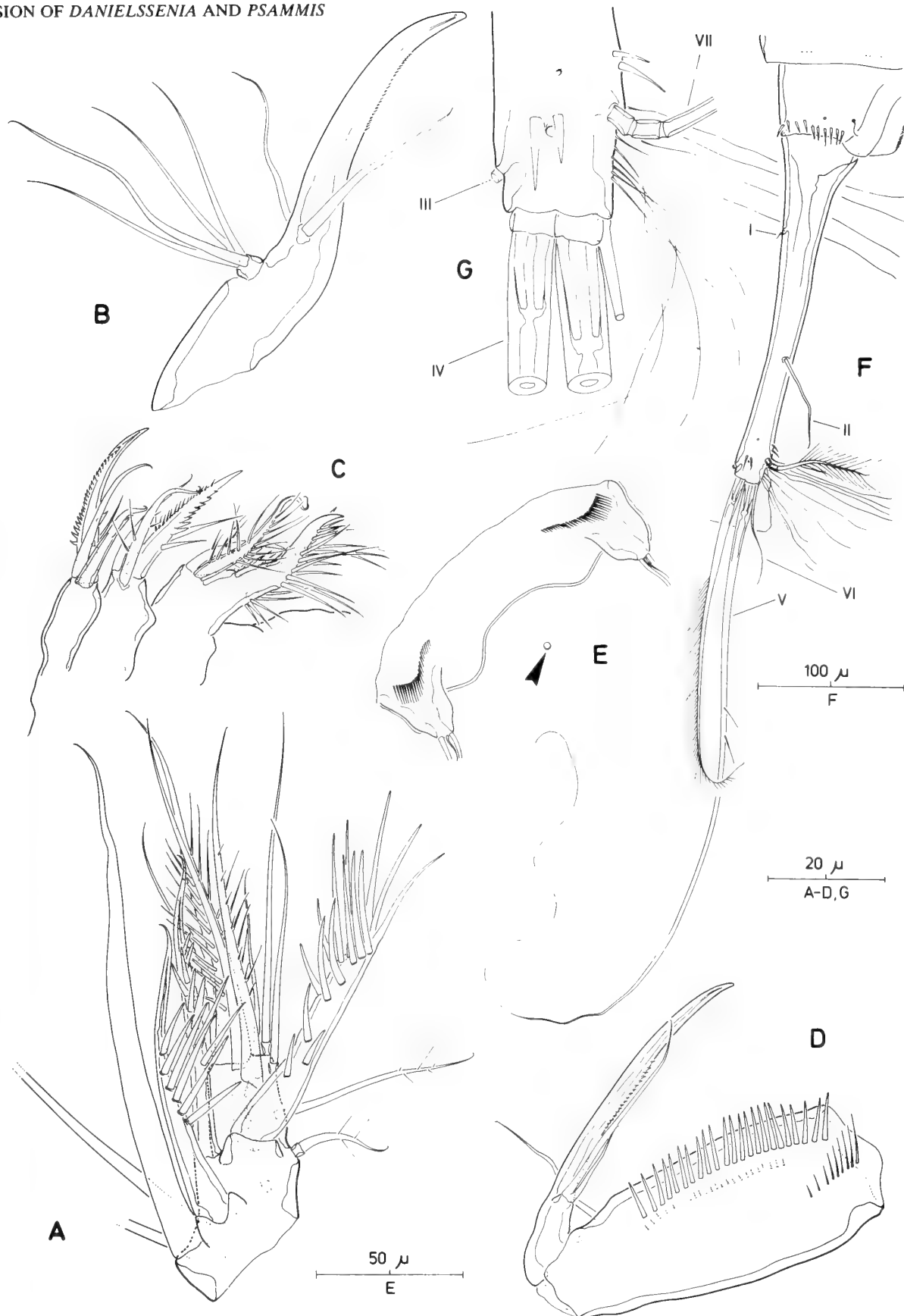


fig. 18 *Bathypsammis longifurca* comb. nov. Female: A, antennule, distal segment; B, maxilla, allobasis and endopod; C, maxilla, syncoxal endites; D, maxilliped, anterior (syncoxa missing); E, genital apertures and copulatory pore (arrowed); F, anal somite and left caudal ramus, dorsal; G, caudal ramus, detail of posterior margin.

longifurca to a new genus *Bathypsammis* which is closely related to *Psammis*.

Genus *Psammis* Sars, 1910

With the removal of *P. longifurca* to *Bathypsammis* gen. nov., the number of species currently allocated to the genus *Psammis* is reduced to four: *P. longisetosa* Sars, 1910; *P. borealis* Klie, 1939; *P. kliei* Smirnov, 1946; and, *P. longipes* Becker, 1974.

(i) *Psammis borealis* Klie, 1939

This species was first briefly diagnosed in 1939 from material collected in deep water near Iceland. A more extensive description, accompanied by illustrations, was published in 1941. Any justification for placing this species in *Psammis* is missing from Klie's (1939, 1941) papers, providing instead a large number of fundamental differences with the type species *P. longisetosa*. We have re-examined Klie's type material of *P. borealis* (Cop. 211–215; 4 ♀♀, 1 ♂, all dissected on slides; Zoologisches Museum der Universität Kiel). The slide of the male is somewhat confusing in that there seems to be 3 mounted antennules which do not show male characteristics and only part of one which does have the features of a male. Further, the limbs on this slide show no sexual dimorphism on either P2 or P3. The genital somite is also missing and the only appendage that differs from the slides of the females is the P5. The fifth legs of both sexes are exactly as drawn in Figs. 4 & 6 in Klie (1941). However, based on the mouthparts and the setation of the female thoracopods, and pending more information on swimming leg sexual dimorphism, we propose to retain this species within the Paranannopidae as *species incertae sedis*. It should be noted here that the specimens labelled *P. borealis* and deposited in the Smithsonian Institution (reg. no. 00231018) by Prof. Dr B.C. Coull are not the same genus as that of Klie (1939). This material (2 ♀♀) collected from the North Carolina continental shelf [this record is not listed in Coull (1971)] closely resembles *Pseudotachidius similis* T. Scott, 1902 and *P. minutus* Itô, 1983.

(ii) *Psammis kliei* Smirnov, 1946

We have been unable to discover the type material of *P. kliei* described by Smirnov (1946) from Henrietta Island (New Siberian Islands, East Siberian Sea). However, the recent recovery of a specimen from Spitsbergen which we believe is referable to this species, indicates that it should be placed in another genus close to *Psammis* and *Danielssenia*. This will be discussed further in a future paper on the Paranannopidae of Spitsbergen (Gee & Huys, in prep.).

(iii) *Psammis longipes* Becker, 1974

MATERIAL EXAMINED. Holotype ♀ dissected on 2 slides (Becker collection; Zoologisches Museum der Universität Kiel, reg. no. 1009–1010); Peru Trough, R/V *Anton Bruun* Sta. 179, 12°03'S 78°45'W, depth 5000 m, leg. W. Noodt.

This species is known from the type locality only. The following redescription (Figs. 19–20) is confined to structures that were misinterpreted or not well illustrated in Becker's (1974) original description:

Mandible (Figs. 19A–B). Gnathobase with multicuspidate, elongate teeth decreasing in size dorsally, and with 2 pinnate

setae near the distal dorsal corner; coxa with large spinules around the base of the palp. Basis with 3 setae, middle one with shorter spinules. Endopod only slightly longer than exopod, with 1 lateral and 3 apical setae; exopod with 1 lateral and 2 apical setae.

Maxillule (Fig. 19C–D). Praecoxal arthrite with 9 pinnate spines and 1 tubular seta around the distal margin and with 2 geniculate tubular setae on the anterior surface. Coxal endite specialized; armature consisting of 3 tubular setae and 3 spines; largest (= anterior) spine with broad base, a comb of flat spinules along the inner margin and ending in a tubular extension; middle spine also swollen at base and with fan of non-articulating flat spinules arranged around the apex; posterior spine with large spinule. Basal endite with 3 plumose setae and 1 short spine with tubular extension. Endopod and exopod with 3 setae each.

Maxilla (Fig. 19E). Praecoxal endite with 2 pinnate spines, distal one with tubular extension. Coxal endites with 2 spines and 1 seta each, distal spine and posterior seta with tubular extension. Allobasis with 2 articulating claws and a tubular seta on either anterior and posterior surface. Endopod with 1 simple and 3 tubular setae.

Maxilliped (Fig. 19F) as described by Becker (1974) except that the endopodal claw bears an accessory seta.

The armature formula given by Becker for the swimming legs is erroneous on two points: P3 enp-2 has only 1 inner seta, the proximal one shown in his figure being an enlarged spinule; P3–P4 exp-3 have an extra element distally, representing the reduced inner terminal seta (Fig. 20A–B).

Fifth leg (Fig. 20C). An incomplete furrow on the posterior surface marks the original proximal margin of the endopodal lobe. The 3 distal setae of this lobe are multipinnate.

Genital field (Fig. 20D) with small copulatory pore leading via linear duct to bilobate seminal receptacle largely located anterior to genital slit. P6 armature represented by pinnate seta and 2 minute spinules (vestigial setae?).

Hyaline frill of all body somites finely dentate; pseudopericulum well developed (Fig. 20E). Pattern of caudal ramus setae as in Fig. 20E.

(iv) *Psammis longisetosa* Sars, 1910

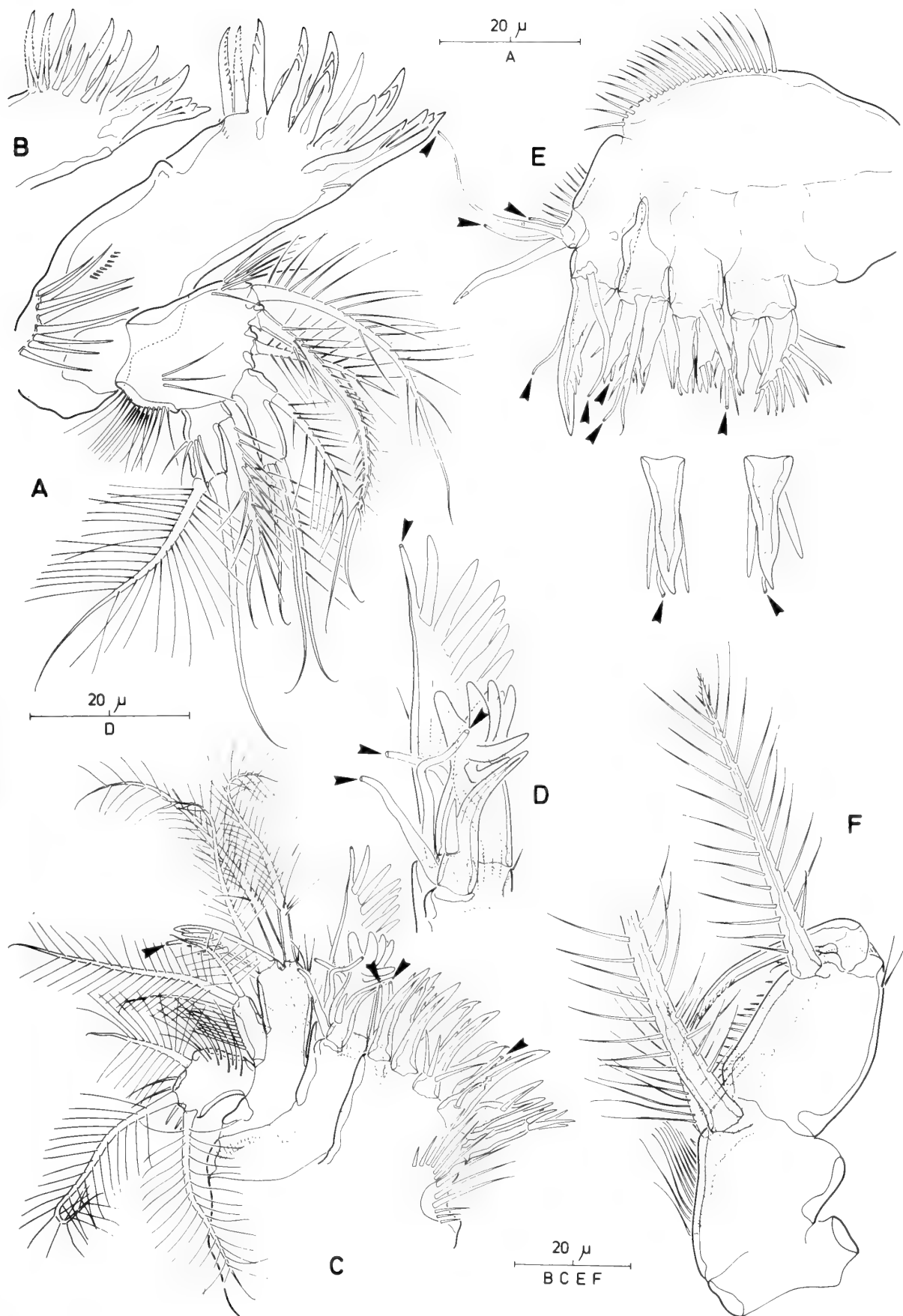
MATERIAL EXAMINED.

— Zoologisk Museum, Oslo: (a) G.O. Sars collection: F20223: 1 ♀ (in alcohol) and 1 ♂ (dissected); collected from Farsund (type locality), Norway; F20224: vial containing 19 ♀♀ and 6 ♂♂; collected from Risør, Norway;

(b) F20929: 4 ♀♀ (2 on slides, 2 in alcohol), 3 ♂♂ (1 on slide, 2 in alcohol); collected by J.A. Berg, deposited by J.M. Gee, from Bjørnehodebukta (59°42.8'N, 10°32.2'E), Oslofjord, 35 m depth, June 1984;

— The Natural History Museum: 1992.1096: 1 ♂ (in alcohol), 1 ♀ (on 6 slides), 1 ♂ prosome (on 7 slides); collected by R. Huys, from Frierfjord-Langesundfjord, 55 m depth, spring 1985.

The original descriptions of *P. longisetosa* given by Sars (1910, 1921) have been supplemented since by a complete redescription by Gee (1988a). The single female collected from Raunefjorden and figured by Por (1965) in all probability does not belong to *P. longisetosa*. In addition to the differences in the shape and armature of the P5 mentioned by Por, substantial discrepancies appear from his illustrations of the P1 (relative proportions of endopodal segments), last



g. 19 *Psammis longipes*. Female: A, mandible, posterior; B, mandible, gnathobase, anterior; C, maxillule, posterior; D, maxillule, detail of coxal endite; E, maxilla, posterior (showing syncoxal spines enlarged); F, maxilliped, posterior. [Tubular setae arrowed in C-E.]

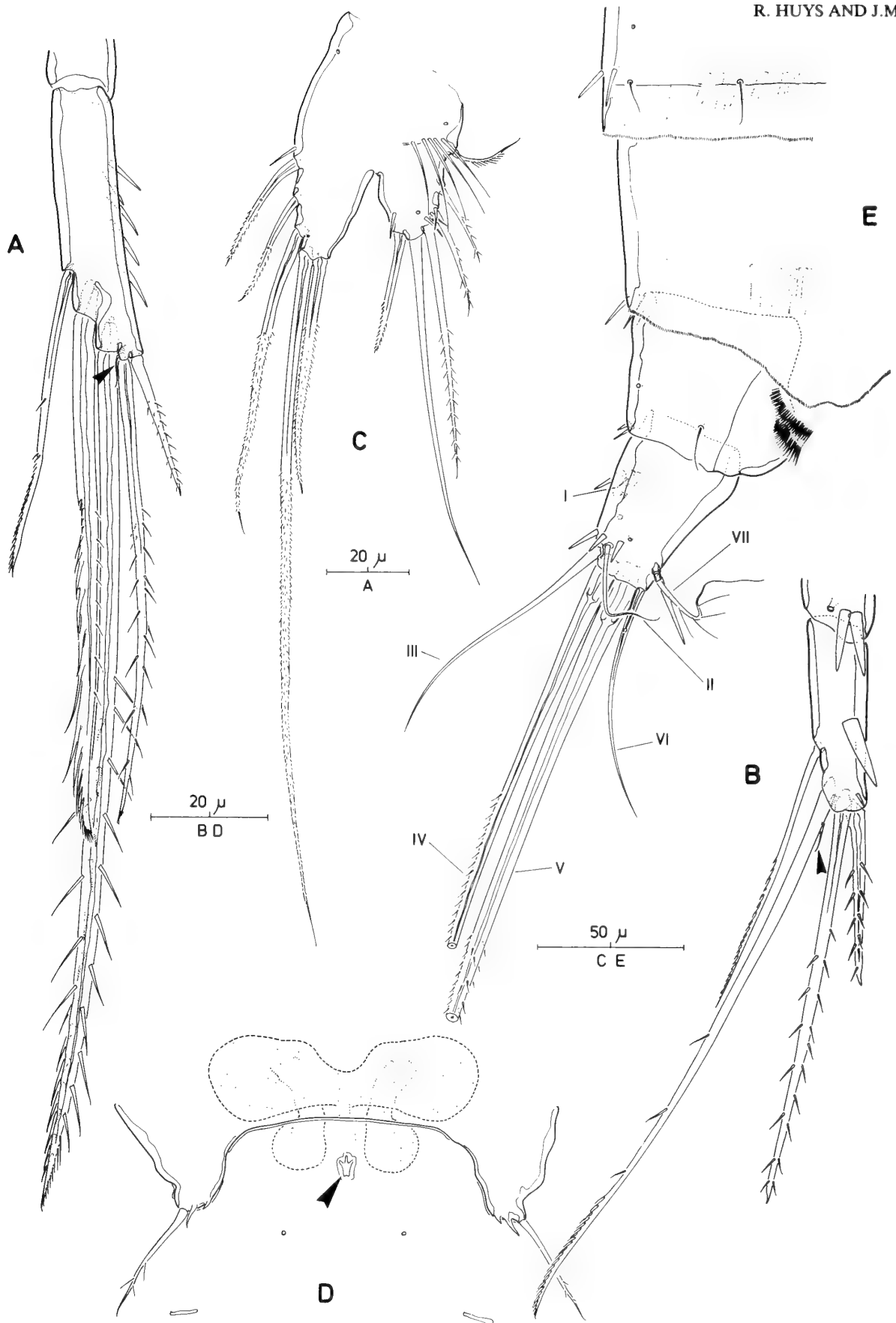


Fig. 20 *Psammis longipes*. Female: A, P3 endopod, distal segment; B, P4 endopod, distal segment; C, P5, anterior; D, genital apertures and copulatory pore (arrowed); E, posterior abdominal somites and left caudal ramus, dorsal. [Vestigial seta arrowed in A-B].

abdominal somites (ornamentation) and caudal rami (shape).

Re-examination of *P. longisetosa* has revealed a number of features that were overlooked or misinterpreted in earlier descriptions. In many cases these observations have shown an astonishing similarity in the detailed structure of the cephalic appendages between *P. longipes* and the type species.

The rostrum is not hyaline (Fig. 22A); the anterior pair of sensillae is enlarged. In the male the antennule is 9-segmented (Fig. 22A) and the segmental pattern is homologous to that of *Archisenia*.

Mandible (Fig. 21A–B). The gnathobase has similar multicuspidate teeth and 2 pinnate setae. The basis has 4 setae; the ornamentation of these setae shows that it is either the proximalmost or following seta that is missing in *P. longipes*. Both species have the same armature on the rami.

Labrum (Fig. 22B) with 1 large, median and a pair of smaller secretory pores on the anterior surface, and long spinules around the distal margin.

The detailed structure of the maxillule and maxilla is exactly the same as in *P. longipes*, including the presence and position of tubular setae and the modifications of the maxillary coxal endite.

The maxillipedal syncoxa has been invariably described as possessing a single, very large, spinulose seta, corresponding to the posterior seta in *P. longipes*; the smaller, setulose, anterior seta in this species is further reduced to a minute, pinnate spine in *P. longisetosa* (arrowed in Fig. 21C) and approaches the length of the largest ornamental spinules, the reason why it had been overlooked in previous descriptions.

The sexual dimorphism on the P2 endopod includes modifications of the middle and distal segments (Figs 21D–E). The anterior, spinous apophysis on the outer margin of the proximal segment is not a sexually dimorphic feature since it is also found in female specimens. The middle segment is drawn out into a large apophysis not reaching to the end of the distal segment and provided with an anterior secretory pore near the apex; the inner margin has 2 distally serrate setae, the proximal one being slightly displaced to the posterior surface; these setae are distinctly longer in the female. The distal segment possesses 4 articulating armature elements corresponding to the 2 inner and 2 terminal setae in the female; the outer spine in the female is modified in the male and replaced by a short, spinous process distally.

As in *P. longipes*, the reduced inner terminal seta of P3–P4 enp-3, represented by a setule, has been overlooked thus far (arrowed in Figs 21F–G). In the male the outer distal corner of the P3 middle segment is transformed into an acutely recurved process (Fig. 21F); the inner seta on this segment is distinctly longer in the female.

The fifth legs of both sexes are as in Figs 22E and F, respectively.

The original segmentation of the female genital double-somite is marked by a transverse chitinous rib dorsally and ventrally (Fig. 22D). The seminal receptacle is relatively small (Fig. 22C); the P6 is represented by 1 plumose seta and 1 small spinule in the female; in the male the sixth legs are fused and symmetrical, and bear 2 naked setae on either side (Fig. 22G).

(v) Amended diagnosis

Only *P. longisetosa* and *P. longipes* are retained in the genus *Psammis*, which is here redefined.

DIAGNOSIS. Paranannopidae. Body large, slightly fusiform and dorso-ventrally flattened. Rostrum not hyaline, with 2 pairs of sensillae, anterior one large. Somatic hyaline frills minutely dentate. Female genital double-somite with lateral and ventral sub-cuticular ridge marking original segmentation; genital field with minute copulatory pore and linear duct leading to transverse seminal receptacle located anterior to genital slit; P6 with 1 plumose seta and 1–2 minute spinulose elements. Pseudopericulum hyaline with dentate margin. Caudal rami divergent and longer than broad, tapering slightly. Female antennule 4-segmented; aesthetasc on segment 3; all segments with pinnate setae and spines. Antennary exopod 3-segmented with armature formula [2–1–3]. Mandibular coxa elongate, with finely pointed teeth and 2 setae on gnathobase; basis broad with 3–4 setae on distal margin; endopod 1-segmented, equal in length to exopod, with strongly reduced armature; exopod 1-segmented, with 1 lateral and 2 distal setae. Maxillule with 2 large comb-like spines and 3 tubular setae on coxal endite; basal endite with 3 plumose setae, 1 spine and 1 tubular seta. Maxilla with tubular setae on coxal endites, allobasis and endopod; praecoxal endite with 2 pinnate spines. Maxilliped subchelate with 1 large and 1 small seta (both pinnate) on syncoxa; basis with long plumose seta on palmar margin, endopodal claw with 1 accessory seta. P1 exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod at least as long as exopod, 2-segmented, enp-2 longer than enp-1, inner seta implanted medially. P2–P4 intercoxal sclerites without ornamentation; rami 3-segmented; exp-1 with an inner seta. P2 endopod distinctly longer than exopod; enp-1 with outer distal margin attenuated in both sexes; enp-2 with 1 inner margin seta and 1 seta implanted on posterior surface. Inner distal seta enp-3 P3–P4 extremely reduced and represented by setule. Armature formula of P1–P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.123	1.2.221
P3	1.1.223	1.1.321
P4	1.1.223	1.1.221

Female fifth pair of legs not fused medially; exopod and baseopod fused to form a bilobate plate; exopodal lobe with 4–5 setae, endopodal lobe with 5 setae.

Male with sexual dimorphism in antennule, P2 endopod, P3 endopod, P5, P6 and in genital segmentation. Antennule 9-segmented, subchirocer; segment 6 swollen, with aesthetasc. P2 enp-2 with long outer apophysis not reaching to distal margin of enp-2; enp-3 with outer spine transformed into non-articulating process, distal setae reduced and inner setae enlarged compared to the female. P3 enp-2 with outer distal corner attenuated into a recurved apophysis. Fifth pair of legs not fused medially; endopodal lobe with 2 spines, exopod with 4 setae/spines. Sixth legs symmetrical, fused to somite, with 2 setae each.

TYPE SPECIES. *P. longisetosa* Sars, 1910 (by monotypy).

OTHER SPECIES. *P. longipes* Becker, 1974.

Gee (1988a) concurred with Wells' (1967) opinion that a generic distinction between *Danielssenia* and *Psammis* on the base of P5 segmentation alone can hardly be justified.

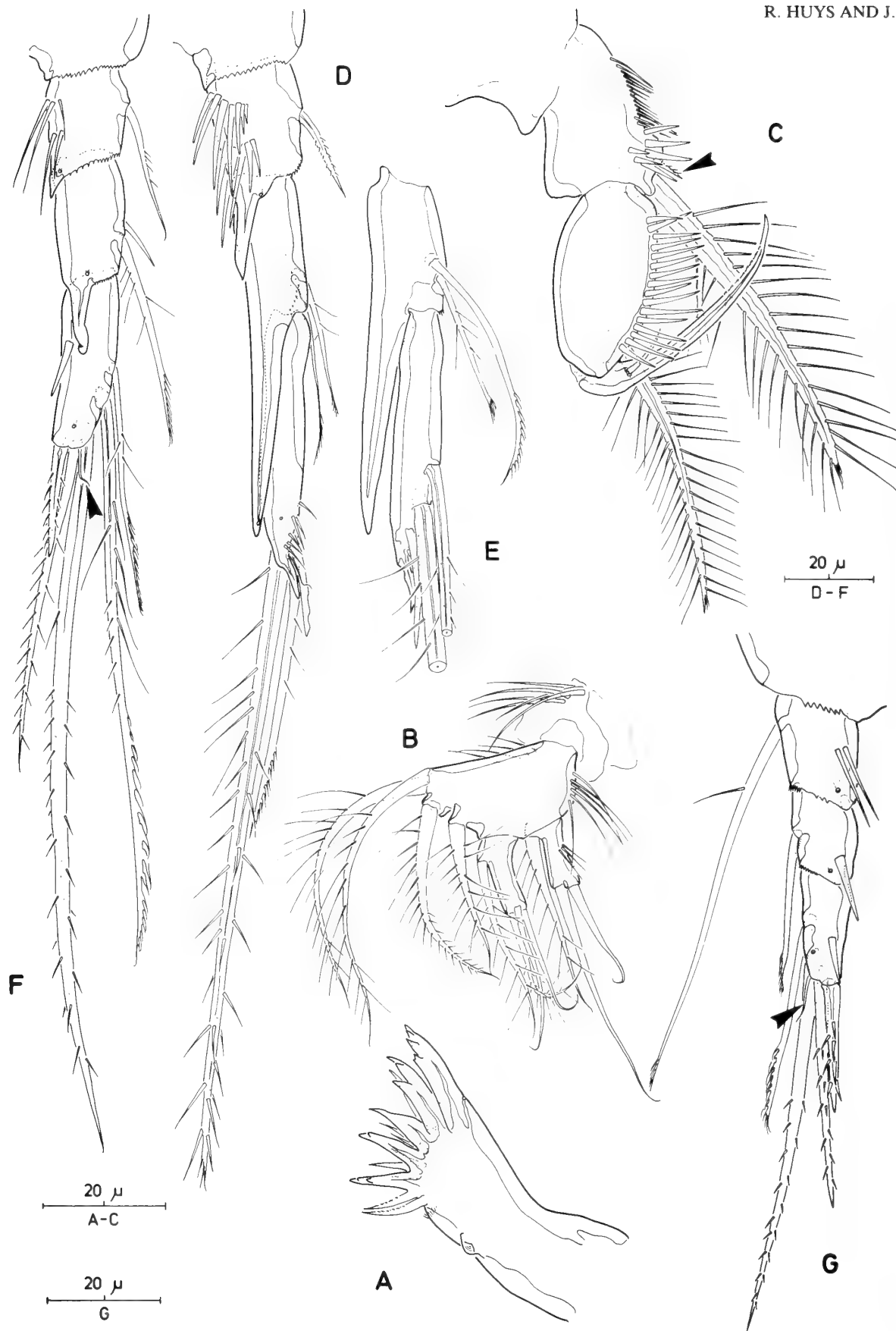


Fig. 21 *Psammis longisetosa*. Female: A, mandible, gnathobase; B, mandible, palp; C, maxilliped, anterior (small seta on syncopa arrowed). Male: D, P2 endopod, anterior; E, P2 endopod, middle and distal segments, posterior; F, P3 endopod (small seta arrowed); G, P4 endopod (small seta arrowed).

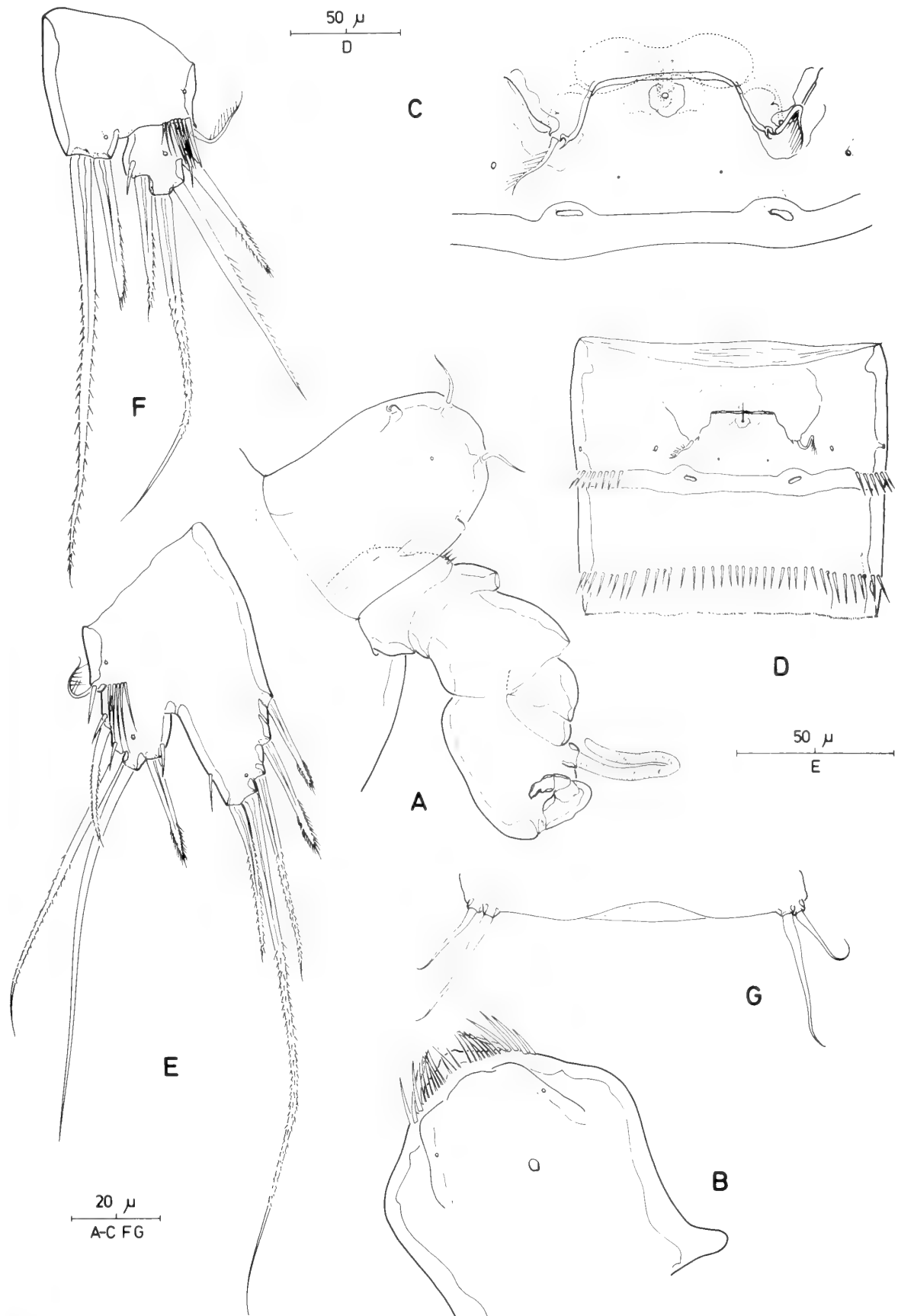


Fig. 22 *Psammis longisetosa*. Male: A, antennule and rostrum (armature omitted); F, P5, anterior; G, P6. Female: B, labrum, anterior; C, genital apertures and copulatory pore; D, genital double-somite, ventral; E, P5, anterior.

However, Gee also pointed out that the mandibular gnathobase in all *Psammis* species bears long, relatively fine, sharply pointed and widely separated teeth compared to the species of *Danielssenia* where these teeth are short, stout, blunt and closely set. On the base of this difference he suggested that both genera probably utilize different food items and to a certain extent are trophically isolated. In combination with the fused rami in the female P5, this evidence was considered as sufficient to maintain *Psammis*' separate generic status. Close examination of the mouthparts in *P. longisetosa* and *P. longipes* and comparison with *D. typica* has now revealed several other characters that can be used to distinguish both genera. Unique features for *Psammis* are the specialized comb-like spines on the coxal endite of the maxillule, the presence of only two spines on the praecoxal endite of the maxilla, and the extremely enlarged, spinulose seta on the maxillipedal basis. The presence of tubular setae and modified spines with tubular extensions on the maxillule and maxilla is a character that is shared by both genera though the precise number is not identical. It is conceivable that these specialized structures might perform a sensory role (as chemo- or probably mechanoreceptors) in remote food detection and/or manipulation. Both genera are predominantly found in the upper flocculent layer of muddy substrates where selection of food-particles probably requires a different mechanism. This could be particularly true for deepwater bottoms (fjords, abyss) where either turbidity is high or the proportion of suspended food-particles might fall below a subsistence level. The unique specialization of the mandibles, maxillules and maxillae might be viewed collectively as the result of a different dietary discrimination mechanism based on successful remote selection of food particles and thus avoiding the unnecessary high energy costs of rejecting unsuitable items upon initial capture. It is noted here that the claviform aesthetascs found on the mouthparts of certain other Paranannopidae (Gee & Huys, 1991) are not homologous to the tubular setae or modified spines bearing tubular extensions.

Another unique apomorphy of *Psammis* is illustrated by the setation pattern on the endopods of P3 and P4 (Fig. 23). The ancestral condition of P3 enp-3 is shown by e.g. *Archisenia* and consists of 1 outer spine (a), 2 distal spines (b-c) and 3 inner setae (d-f). This full complement of armature elements is also found in *Psammis* but is obscured by modifications in the distal part of the segment. The extreme reduction of the inner terminal spine (c) and the distad displacement of the distal inner seta (d) are the main reasons why the setal formula was erroneously cited as 221 (or 121 in P4) in previous descriptions. The distal elements expressed in this formula are b and d, rather than b and c. The spiniform and pinnate nature of seta d in *Psammis* did certainly contribute to this misunderstanding. The reduced condition in *Bathypsammis* (Fig. 23) has not evolved from the *Psammis* pattern but resulted through the loss of 2 inner setae. It is impossible to determine which seta (d, e or f) has been retained in *B. longifurca*.

Both species of *Psammis* can be differentiated by the number of setae on the mandibular basis (3 in *longipes*, 4 in *longisetosa*), the length of the anterior seta on the syncopa which is distinctly longer in *P. longipes*, the ratio of endopod length to exopod length in P1 to P3 being much higher in *P. longipes*, the number of setae on the ♀ P5 exopod (4 in

longisetosa, 5 in *longipes*), and the gross difference in body size ($\pm 550 \mu\text{m}$ in *longisetosa*, $\pm 900 \mu\text{m}$ in *longipes*).

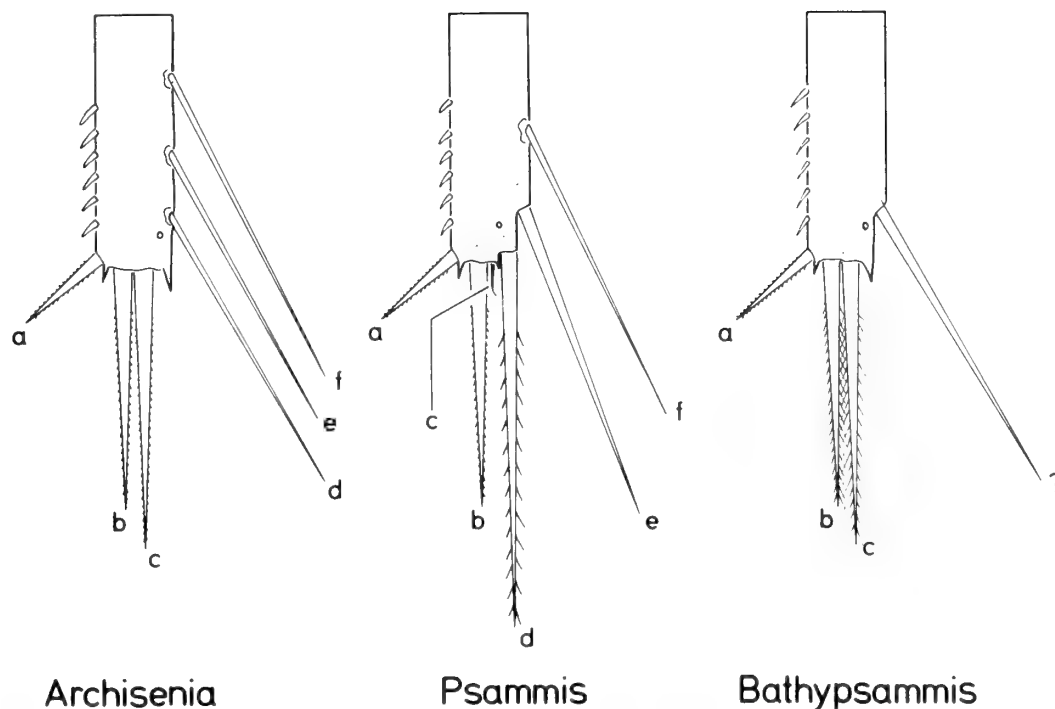
DISCUSSION

Within the Paranannopidae, aesthetascs on the mouthparts are a powerful synapomorphy for separating a number of genera which have recently been created or redefined, viz. *Jonesiella* (cf. Huys & Gee, 1992), *Paradanielssenia*, *Micropsammis*, *Telopsammis* and *Leptotachidia* (cf. Gee & Huys, 1991), *Sentiropsis* and *Peltisenia* (Huys & Gee, in press). The absence of such sensory appendages in *Archisenia* excludes it from this lineage and allies it with the more primitive danielsseniid genera, namely *Fladenia*, *Danielssenia*, *Psammis* and *Bathypsammis*. However, the phylogenetic relationships amongst these more primitive danielsseniid genera are somewhat unclear at the moment particularly with respect to the position occupied by *Archisenia*. The problem is that this genus shows a mosaic of primitive plesiomorphic characters (6-segmented female antennule; setal formula of legs P2-P4 with 7.8.8 setae/spines on exp-3 and 5.6.5 setae on enp-3; P5 with 5 setae on baseoendopod and exopod), but at the same time a number of unique autapomorphies in the sexual dimorphism on P1 basis, P2 enp-1 and P3 enp-2.

Within this group of genera it is clear that *Fladenia* is the most primitive genus because it retains both vestiges of sexual dimorphism involving a difference in the number of elements (in this case setae) on the endopod of P3 and P4 (Gee & Huys, 1990) and a primitive setal formula particularly in the exopods of P3 and P4. It is also clear that *Danielssenia*, *Psammis* and *Bathypsammis* are linked by a 4-segmented female antennule, a reduced number of setae on P4 enp-3 and probably by having only 2 setae on the P6 in the male (though the latter character cannot be scored for *Bathypsammis* since the male is unknown). Since it has no vestige of P3 and P4 setal sexual dimorphism and does not show the apomorphies of the *Danielssenia* lineage, it is likely that *Archisenia* diverged from the main evolutionary line after *Fladenia* and probably before the *Danielssenia*-grouping.

Within the *Danielssenia*-*Psammis*-*Bathypsammis* lineage, *Danielssenia* is considered the most advanced genus on account of the loss of a seta on exp-1 of the antenna, the basis of the mandible, exp-1 of P2-P4 and enp-2 of P2. Unique apomorphies for this genus are the typically ventrally deflected rostrum, the blunt teeth on the mandibular gnathobase, and the dorsal, incised, hyaline frill on the P5-bearing somite. Another diagnostic character for *Danielssenia* is illustrated by the shape of the seminal receptacle. Multi-chambered receptacles have been described for a number of Paranannopidae such as *Leptotachidia*, *Telopsammis*, *Psammis* and *Paranannopus* (Gee & Huys, 1990, 1990) and might well be the ancestral state in this family. However, in none of these genera the paired anterior chambers are elongate, cylindrical reservoirs extending into the posterior part of the P5-bearing somite.

Analysis of the precise relationships within the *Danielssenia* grouping is hampered by the absence of male *Bathypsammis*. The specialized tubular structures on the endites of the maxillule and maxilla provides a robust synapomorphy to link *Danielssenia* and *Psammis*. A close relationship is also indicated by the armature of the female sixth legs bearing one



Archisenia

Psammis

Bathypsammis

Fig. 23 Comparison of armature on distal endopod segment of P3 in *Archisenia*, *Psammis* and *Bathypsammis*.

plumose seta and 2 inner, minute spiniform elements (compared to 2 setae and 1 setule in between in *Bathypsammis*), and by a detailed comparison of the distal transformations in the male P2 endopod. Potential synapomorphies grouping *Psammis* and *Bathypsammis* are: (i) rostrum with enlarged anterior sensillae; (ii) the mandibular exopod with only 1 lateral and 2 apical setae; (iii) the fusion of the exopod and baseoendopod in the female P5. Some species of *Danielssenia*, however, also show a reduction in the setation of the mandibular exopod (e.g. *D. typica*), and the fused P5 in *Bathypsammis* might have been evolved convergently, since, in other respects, it is very different from the condition in *Psammis*. The rostral character might also be a product of convergence since the enlargement of the anterior pair of sensillae has evolved independently in a number of other deepwater genera such as *Paranannopus* and *Cylindronannopus*.

Unique apomorphies for *Psammis* are: (i) reduction of the mandibular endopod (1 lateral, 3 apical setae); (ii) the specialized comb-like spines on the maxillary coxal endite; (iii) praecoxal endite of maxilla with only 2 spines; (iv) extreme development of the posterior seta on the maxillipedal basis; (v) elongation of P2 endopod, being longer than the exopod; (vi) the apophysis on P2 enp-1 in both sexes; (vii) reduction of the inner terminal seta on P3–P4 enp-3. In *Bathypsammis* the unique apomorphies are confined to the female as the male is unknown: (i) a very long outer basal seta on the basis of P1; (ii) a very long caudal ramus with a plume of setules on the inner distal corner; (iii) the form of the setae on the endopodal lobe of the female P5.

KEY TO GENERA OF PARANANNOPIDAE

REMARK. This key also includes *Psammis kliei* Smirnov, 1946, which will be placed in a genus by itself in a forthcoming paper (Gee & Huys, in prep.), and the genus *Carolinicola* Huys & Thistle, provisionally assigned to the Paranannopidae by Huys & Thistle (1989).

1. P4 endopod 3-segmented 4.
P4 endopod 2-segmented, 1-segmented or absent 2.
2. Antennary exopod 1-segmented
..... *Carolinicola* Huys & Thistle, 1989.
Antennary exopod 3-segmented 3.
3. Body short, robust; caudal rami setae IV and V long and spinulose; P5 well developed, covering entire width of thoracic somite
..... *Paranannopus* Lang, 1936.
Body slender, cylindrical to vermiform; caudal rami setae IV and V short and plumose; P5 a minute plate, located midventrally *Cylindronannopus* Coull, 1973.
4. P2–P4 exp-1 without inner seta 5.
P2–P4 exp-1 with inner seta 7.
5. Antennules without plumose or pinnate spines/
setae *Sentiopsis* Huys & Gee, 1993.
Antennules with plumose and/or pinnate spines/setae 6.
6. Caudal ramus with distinct cluster of long setules at the inner distal corner; P2 enp-2 with large apophysis in ♀ (and presumably in ♂ also) *Psammis kliei* Smirnov, 1946.
Caudal ramus without such cluster; P2 enp-2 with large apophysis in ♂ only *Danielssenia* Boeck, 1872.
7. P4 exp-3 with 8 setae/spines 8.
P4 exp-3 with at most 7 setae/spines 13.
8. P2 enp-2 with 2 inner setae 9.

- P2 enp-2 with 1 inner seta 10.
9. Caudal rami 5 times as long as maximum width; P1 endopod shorter than exopod; P5 ♀ with fused exopod and baseoendopod *Bathypsammis* gen. nov. Caudal rami broader than long; P1 endopod longer than exopod; P5 ♀ with separated exopod and baseoendopod *Jonesiella* Brady, 1880.
10. Body dorsoventrally flattened; caudal rami setae IV and V stubby and spiniform; P1 enp-1 1.5 times as long as enp-2 *Peltisenia* Huys & Gee, 1993. Body not dorsoventrally flattened; caudal rami setae IV and V long and setiform; P1 enp-1 at most as long as enp-2 11.
11. Antennule ♀ 4-segmented; club-shaped aesthetascs present on mandible (endopod), maxillule (basis) and maxilla (endopod); P2 enp-2 ♂ without distinct outer apophysis *Paradanielssenia* Soyer, 1970. Antennule ♀ 6-segmented; no club-shaped aesthetascs on mouthparts; P2 enp-2 ♂ with long outer apophysis 12.
12. Antennary exopod with 1 seta on proximal segment; P3 exp-3 with 7 setae/spines; P2 enp-3 with inner distal seta transformed into large pinnate spine reaching beyond apophysis of enp-2 *Afrosenia* Huys & Gee, 1993. Antennary exopod with 2 setae on proximal segment; P3 exp-3 with 8 setae/spines; P2 enp-3 ♂ with inner distal seta not transformed and shorter than apophysis of enp-2 *Archisenia* gen. nov.
13. P2 enp-2 with 2 inner setae *Psammis* Sars, 1910. P2 enp-1 with 0–1 inner setae 14.
14. Club-shaped aesthetascs present on mandible (endopod), maxillule (basis) and maxilla (endopod); P2 exp-3 with at most 6 setae/spines 15. No club-shaped aesthetascs present on these appendages; P2 exp-3 with 7 setae/spines *Fladenia* Gee & Huys, 1990.
15. P1 enp-2 with 2 terminal setae geniculate; P5 ♀ baseoendopod and exopod indistinguishable, with 5 setae; P2 enp-2 ♂ without apophysis; P6 ♂ with 2 setae 16. P1 enp-2 with 1 terminal seta geniculate; P5 ♀ baseoendopod and exopod lobes indistinguishable, with 3 and 4 setae, respectively; P2 enp-2 ♂ with small apophysis; P6 ♂ with 3 setae *Micropsammis* Mielke, 1975.
16. Antennule in both sexes with densely opaque, bulbous appendage on distal segment P2–P4 exp-2 without inner seta *Leptotachidia* Becker, 1974. Antennule in both sexes without densely opaque, bulbous appendage on distal segment P2–P4 exp-2 with inner seta *Telopsammis* Gee & Huys, 1991.

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A new species of *Syrticola* Willems & Claeys, 1982 (Copepoda: Harpacticoida) from Japan with notes on the type species

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SYNOPSIS. A new species of *Syrticola* Willems & Claeys, 1982 (Harpacticoida: Cylindropsyllidae) is described from Okinawa, Japan. Morphological notes on the type species *S. flandricus* Willems & Claeys, 1982 and a key to the species are given. The inadequately described *S. trispinosus* A. Scott, 1896 is ranked as *species inquirenda*. The diagnosis of the genus is amended and its position in the Cylindropsyllidae re-assessed. Both sexes of *S. intermedius* sp. nov. were found to be infested by early parthenogenetic female stages of an as yet undescribed genus of Tantulocarida.

INTRODUCTION

The interstitial harpacticoid fauna of Japan is very poorly known, as is that of most east Asian countries. The paucity of data on marine interstitial species stands in marked contrast with the number of studies on subterranean copepods produced by workers like Miura and Takashi Ito. In fact, with the possible exception of *Microsetella norvegica* (Boeck, 1864) only 11 genuinely interstitial harpacticoids have been recorded from marine and brackish water habitats in Japan (Table 1) and the majority of these was described by the latter author's namesake, the late Tatsunori Itô, whose activities were mainly focussed on the fauna from Hokkaido in the north and the Bonin Islands in the southeast. The only other information on mesopsammic harpacticoids is contained in the papers of Kikuchi (1970, 1972) and Kikuchi & Yokota (1984), reporting on species from Lake Hinuma, a brackish lagoon near the central east coast of the Japanese mainland.

In the course of a survey of the sandy bottom copepods off Nagannu Island, Okinawa (Ryukyu Archipelago) by one of us (S.O.), several interstitial harpacticoids were found to be infested with tantulocaridans (Huys *et al.*, in preparation). This paper describes a new species of *Syrticola* Willems & Claeys (Cylindropsyllidae) based on two specimens that were parasitized by parthenogenetic females of an as yet undescribed tantulocarid.

MATERIALS AND METHODS

Specimens of *Syrticola intermedius* sp. nov. were collected by dredging of a sandy bottom off Nagannu Island, Okinawa, South Japan (26° 14' N, 127° 32' E, depth 46.49 m; leg. S. Ohtsuka) on 9 April 1992. The dredge (mouth area: 50 cm wide x 15 cm high; mesh size 5 mm) was towed along the bottom at a speed of 2 knots by the T/V Toyoshio-maru of the Hiroshima University for about 5 minutes. Copepods were

Table 1 Interstitial harpacticoid copepods reported from marine localities in Japan.

Species	Locality	Reference
ECTINOSOMATIDAE		
<i>Microsetella norvegica</i> (Boeck, 1864)	Hokkaido	Itô (1968)
<i>Arenosetella bidentata</i> Itô, 1972	Hokkaido	Itô (1972, 1984)
<i>Noodtiella</i> sp.	Hokkaido	Itô (1984)
DARCYTHOMPSONIIDAE		
<i>Leptocaris brevicornis</i> (van Douwe, 1904)	Lake Hinuma ¹	Kikuchi & Yokota (1984)
PARAMESOCHRIDAE		
<i>Paramesochra</i> sp.	Hokkaido	Itô (1984)
LEPTASTACIDAE		
<i>Cerconeotes japonicus</i> (Itô, 1968)	Hokkaido	Itô (1968, 1984)
<i>Paraleptastacus unisetosus</i> Itô, 1972	Hokkaido	Itô (1972, 1984)
CYLINDROPSYLLIDAE		
<i>Arenopontia ishikariana</i> Itô, 1968	Hokkaido	Itô (1968, 1984)
<i>Arenopontia sakagami</i> Itô, 1978	Bonin Islands	Itô (1978)
<i>Stenocaris intermedia</i> Itô, 1972	Hokkaido	Itô (1972)
<i>Psammopsyllus imamura</i> Kikuchi, 1972	Lake Hinuma ¹	Kikuchi (1972)
PARASTENOCARIDIDAE		
<i>Parastenocaris hinumaensis</i> Kikuchi, 1970	Lake Hinuma ¹	Kikuchi (1970)

¹ Brackish lagoon.

fixed and preserved in 10% neutralized formalin/sea-water. Females of *S. flandricus* Willems & Claeys, 1982 were collected by the senior author in different localities along the coast of The Netherlands in the course of the biological monitoring programme BIOMON. All specimens have been deposited in the collections of The Natural History Museum, London.

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). All drawings have been prepared using a camera lucida on a Leitz Diaplan differential interference contrast microscope. The descriptive terminology is adopted from Huys & Boxshall (1991). Abbreviations used in the text are: P1–P6, first to sixth thoracopod.

DESCRIPTIONS

Family Cylindropsyllidae

Subfamily Leptopontiinae Lang, 1948

The genus *Syrticola* was established by Willems & Claeys (1982) to accommodate the type species *S. flandricus* Willems & Claeys, 1982 and *Tetragoneiceps trispinosus* A. Scott, 1896. Previously, the latter species had been considered 'species incerta' in the genus *Evansula* T. Scott and thus placed in the subfamily Cylindropsyllinae (Lang, 1948). The close relationship between *Syrticola* and *Notopontia* Bodiou noted by Willems & Claeys (1982) was already hinted at by Bodiou (1977) who recognized a certain resemblance between *T. trispinosus* and *N. stephanieae* Bodiou, 1977, and indirectly also by Mielke (1982) who described (?) *N. galapagoensis*, a

species provisionally placed in *Notopontia* but subsequently allocated to *Syrticola* (Bodiou & Colomines, 1986; Willems *et al.*, 1987). However, none of these authors has formally assigned either of these genera to any of the subfamilies of the Cylindropsyllidae recognized at that time. The only attempt was that by Bodiou (1977) who suggested that *Notopontia* is closest to *Evansula* (Cylindropsyllinae) but to a certain extent is also related to *Arenopontia* Kunz and *Leptopontia* T. Scott (Leptopontiinae).

Lang (1948) subdivided the family into the Cylindropsyllinae, Leptastacinae and Leptopontiinae and a fourth subfamily, the Psammopsyllinae, was added by Krishnaswamy (1956). Recently, the Leptastacinae has been upgraded to full family status (Huys, 1993). The diagnostic sexual dimorphism displayed on thoracopods 2 and 3 by all genera of the Cylindropsyllinae excludes *Notopontia* and *Syrticola* from this subfamily since their swimming leg sexual dimorphism is only slightly developed (and therefore might well have been overlooked in *Notopontia* for which it has been recorded as being completely absent). A detailed comparison with the Leptopontiinae, currently encompassing *Arenopontia*, *Pararenopontia* Bodiou & Colomines and *Leptopontia*, reveals a suite of apomorphic characters supporting a sister-group relationship between *Leptopontia* and the *Notopontia*-*Syrticola* lineage. These characters include: (i) anal operculum drawn out into spinous process(es); (ii) outer distal corner of caudal ramus produced into backwardly directed spinous process; (iii) first antennular segment extremely elongated, much longer than second; (iv) mandibular gnathobase stylet-like with teeth along one side; (v) distal exopod segment P1 with 3 armature elements (proximal outer spine lost); (vi) middle exopod segment P1 without outer spine (in *Syrticola* and *Notopontia* the middle and distal segment are fused or have failed to separate); (vii) apical spines of distal exopod segments P3–P4 setiform; (viii) sexual

dimorphism endopod P3 involving fusion of distal spine to segment; (ix) P5 exopod with 3 elements in both sexes. There is little evidence that *Arenopontia* and *Pararenopontia* share a close relationship with this core group, however pending a revision of these genera it is preferable to retain them in the Leptopontiinae.

Syrticola Willems & Claeys, 1982

DIAGNOSIS (AMENDED). Leptopontiinae. Body cylindrical, but not particularly vermiform. Hyaline frill of all body somites incised. Antennule 6- or 7-segmented in ♀. Maxilla with one syncoxal endite. Midventral spinous process anterior to intercoxal sclerite of P1. P1 exopod 2-segmented. Distal segment P1 endopod with 1 geniculate seta and 1 claw. Distal segment P3–P4 exopods with 1 outer spine. P2–P4 endopods 1-segmented in ♀, P3 endopod 1- or 2-segmented and sexually dimorphic in ♂. P5 with fused baseoendopod and exopod in both sexes; endopodal lobe drawn out into triangular process with 0–1 seta, exopodal lobe a tubercle with 3 elements. Genital apertures not fused in ♀. Anal operculum with a series of small spinous processes or one large median spike. Caudal ramus seta III inserted proximal to seta V.

TYPE SPECIES. *Syrticola flandricus* Willems & Claeys, 1982

OTHER SPECIES. *S. trispinosus* (A. Scott, 1896), *S. galapagoensis* (Mielke, 1982), *S. mediterraneus* Willems *et al.*, 1987, *S. intermedius* sp. nov.

Syrticola intermedius sp. nov. (Figs. 1–4, 5A–C, 6)

MATERIAL EXAMINED. Holotype ♀ dissected on 8 slides, deposited under reg. no. 1992.1075. Paratype ♂ dissected on 6 slides, deposited under reg. no. 1992.1076. Drawings based on the paratype are Figs. 2E–F, 4D–F, 5A–C, 6A–G; all others were drawn from the holotype ♀.

FEMALE. Body length measured from tip of rostrum to posterior margin of caudal rami 485 µm (Figs. 1A–B). Maximum width 75 µm measured at rear margin of cephalothorax. Integument pitted. Pleural areas of cephalothorax not well developed so that appendages are clearly exposed in lateral aspect (Fig. 1B). Posterior margin of body somites (except cephalothorax and anal somite) fringed dorsally and laterally with finely incised hyaline frill; this frill also present ventrally on genital double-somite and abdominal somites (Figs. 1B, 4A–B). Abdominal somites also with transverse spinular row in anterior half which is usually concealed beneath the hyaline frill of the preceding somite as shown in Fig. 5A.

Rostrum triangular, with 2 delicate sensillae (as in male, Fig. 6B).

Genital double-somite (Fig. 4B) about as long as wide; original segmentation not marked by any external or internal cuticular structure; anterior margin with 2 transverse spinular rows. Genital apertures located in anterior quarter of genital double-somite, closely set together but separate and each closed off by small operculum derived from sixth leg; no armature observed but posterior margin of operculum with minute spinous processes and a circular scar at the outer distal corner (probably indicating insertion site of long seta as in *S. flandricus*, cfr. Fig. 5G). Copulatory pore located far anteriorly between genital apertures (arrowed in Fig. 4B). Seminal receptacles not confirmed. Paired widely separated secretory pores at about 2/5 distance from anterior margin.

Anal somite (Figs. 1A–B; 4A; 5A–B) with dorsal operculum drawn out into median, posteriorly directed, spike; process about as long as anal somite proper; ventral posterior margin spinulose medially.

Caudal rami (Figs. 4A; 5A–B) divergent; outer distal corner drawn out into backwardly directed, acutely recurved, spinous process; with 7 setae; seta I minute, setae II and III located anterior to seta I, seta IV tiny and located between spinous process and large seta V, seta VII long and tri-articulate at base, seta VI minute.

Antennule (Fig. 2A) 7-segmented, articulating on a small pedestal as in the male (Fig. 6B); slender, anteriorly directed (Fig. 1A); first segment extremely elongate, about 4 times as long as maximum width, with 1 short seta distally; aesthetasc on fourth segment fused basally to long seta; distal 2 setae of last segment fused basally. All setae bare; setal formula: [1, 8, 3, 2+ae, 1, 2, 9].

Antenna (Figs. 2B–D). Coxa small, not ornamented. Basis and proximal endopod segment fused to form allobasis, original segmentation marked by internal chitinous rib anteriorly and incomplete suture line posteriorly near exopod; basis with serrate seta located on inner lateral surface; exopod small, 1-segmented, with 1 small, apical seta; free endopod articulating with allobasis at right angle (Fig. 1B), lateral margin with 2 spines, distal margin with 1 pinnate spine and 4 geniculate setae, the largest of which is fused basally with vestigial seta and bearing coarse spinule at about midway.

Labrum (Fig. 5C) a ventrally projected, elongate, membranous outgrowth, distinctly tapering distally. Paragnaths small membranous lobes.

Mandible (Figs. 2E–F) with conspicuous coxa, drawn out to form a slender, stylet-like gnathobase bearing small teeth and a long serrate seta near the apex. Palp elongate, 2-segmented; proximal segment representing basis, slightly sigmoid, swollen in distal half, with 1 seta and spinular row; distal segment representing endopod, with 2 lateral and 3 apical setae.

Maxillule (Fig. 2G). Praecoxa with large, cylindrical arthrite bearing 2 anterior surface setae and 6 setae along the distal margin; coxal endite with 2 setae; palp representing fused basis and rami; exopod, endopod, proximal and distal basal endites represented by 1, 2, 2 and 3 setae, respectively.

Maxilla (Fig. 2H) reduced, 2-segmented. Syncoxal with single endite bearing unipinnate seta and conspicuous aesthetasc-like structure representing modified seta with chitinized dorsal margin and tubular membranous part ventrally; exit of maxillary gland discernible in proximal half. Allobasis drawn out into pinnate claw bearing serrate seta at its base. No trace of endopod.

Maxilliped (Fig. 4F) subchelate. Syncoxal and basis without armature but with 3 spinular rows each. Endopod represented by strong claw bearing tiny spinules along distal half of inner margin; an accessory setule is located at the base of the claw.

P1 (Fig. 3A). Praecoxa a small sclerite located around the outer lateral margin of the limb base. Intercoxal sclerite a minute rounded plate. Coxa with spinular row. Basis with inner and outer basal seta and with spinules at middle distal margin. Exopod 2-segmented, proximal segment with blunt spine bearing long setules, distal segment with 2 geniculate setae and 1 unipinnate spine. Endopod 2-segmented, elongate, prehensile; proximal segment about twice as long as exopod, with serrate inner seta near proximal margin; distal segment with 1 geniculate seta, 1 short claw and a patch of

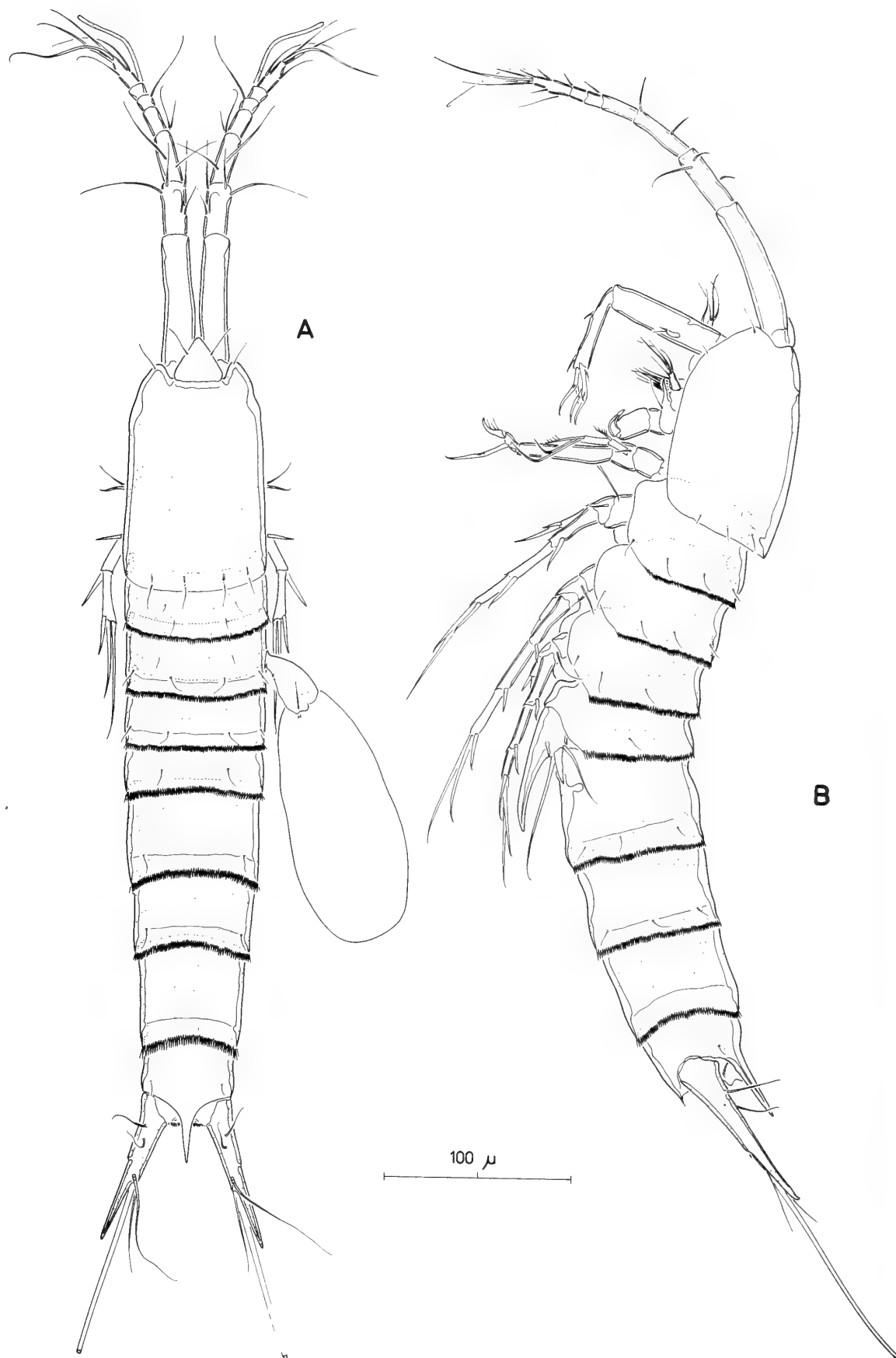
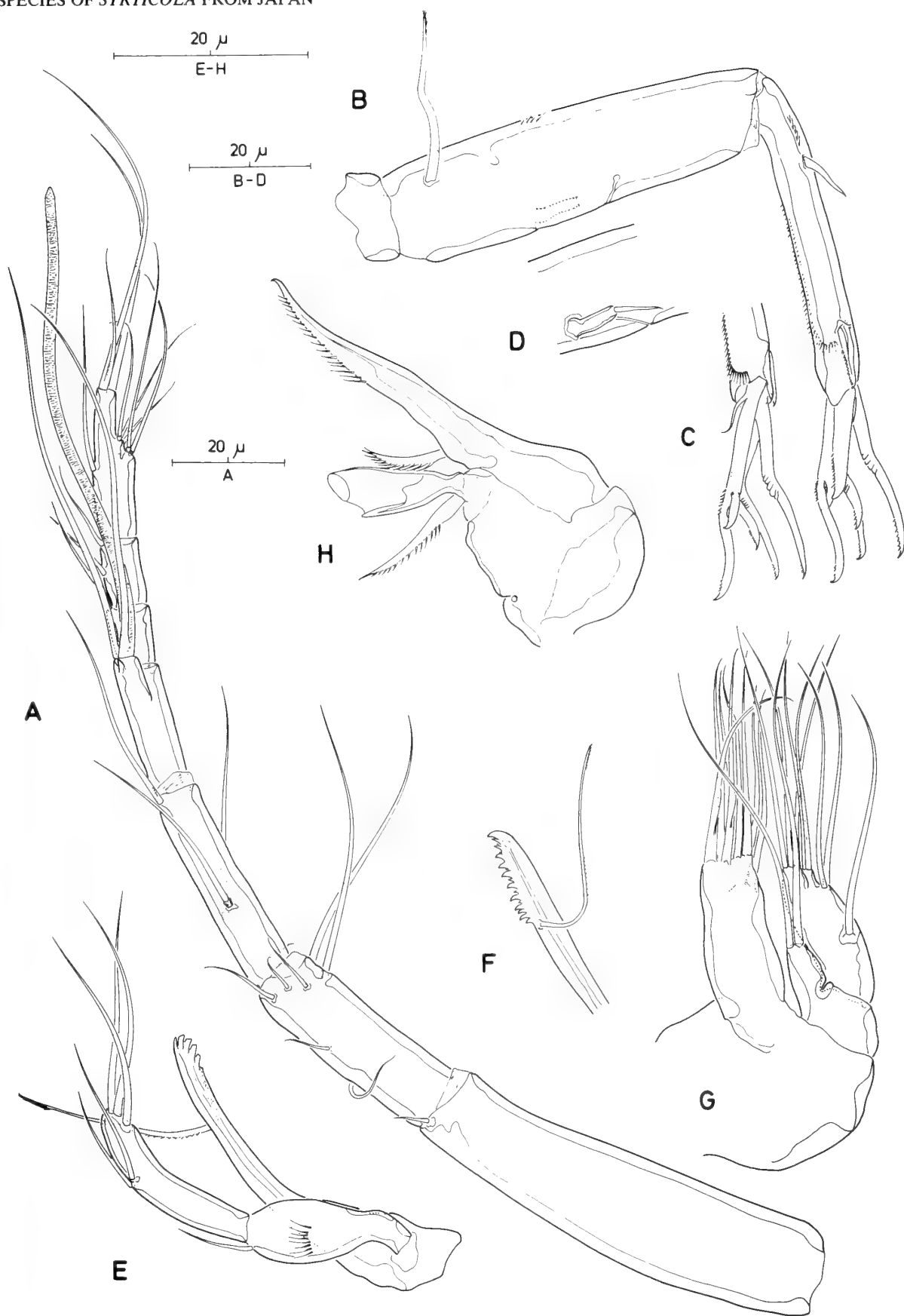


Fig. 1 *Syrticola intermedius* sp. nov. female. A, Habitus, dorsal; B, same, lateral.



g. 2 *Syrticola intermedius* sp. nov. female. A, Antennule; B, antenna, inner lateral view; C, distal end of antennary endopod, outer lateral view; D, antennary exopod, outer lateral view; G, maxillule; H, maxilla. Male. E, mandible; F, Mandible, gnathobase.

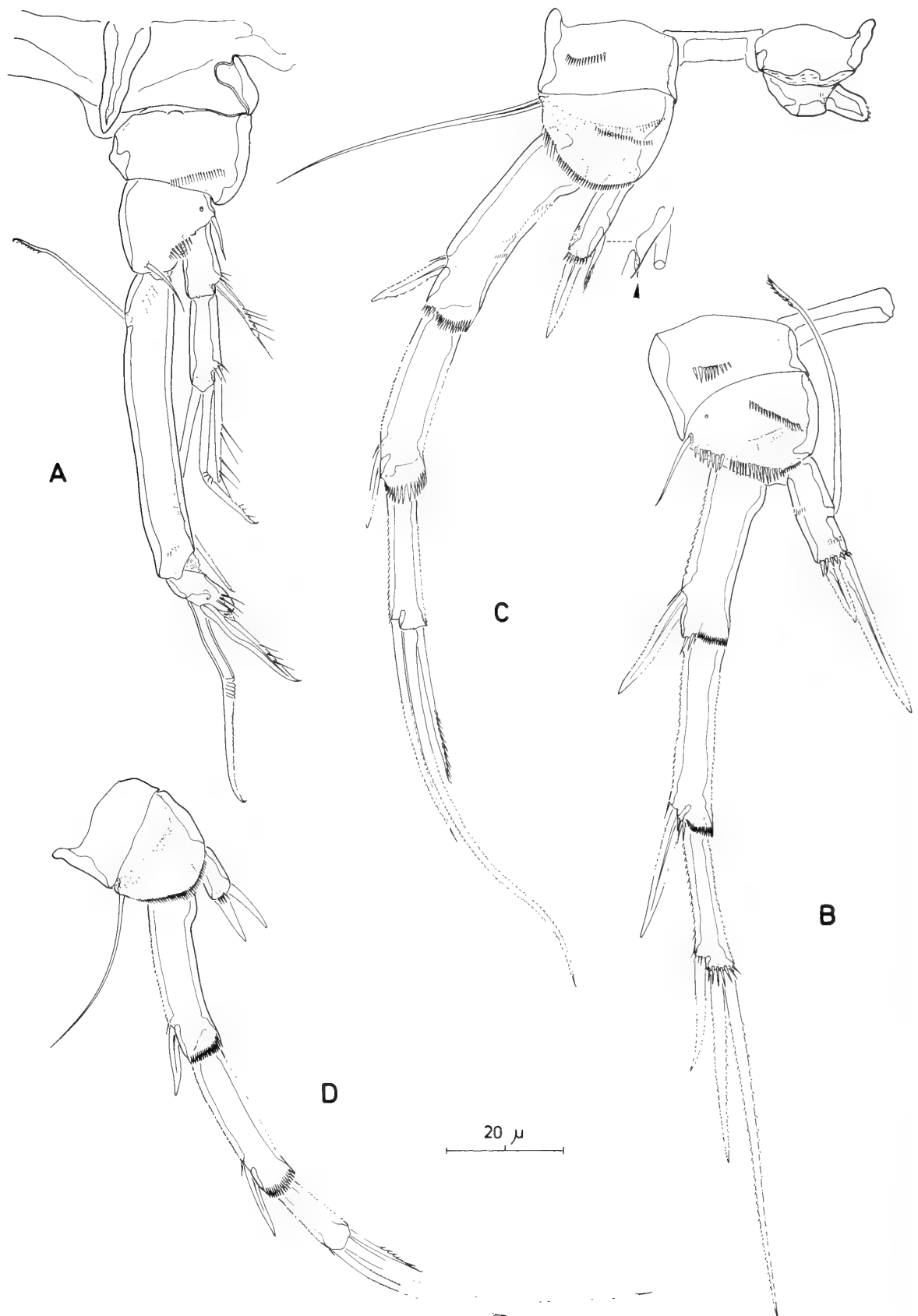
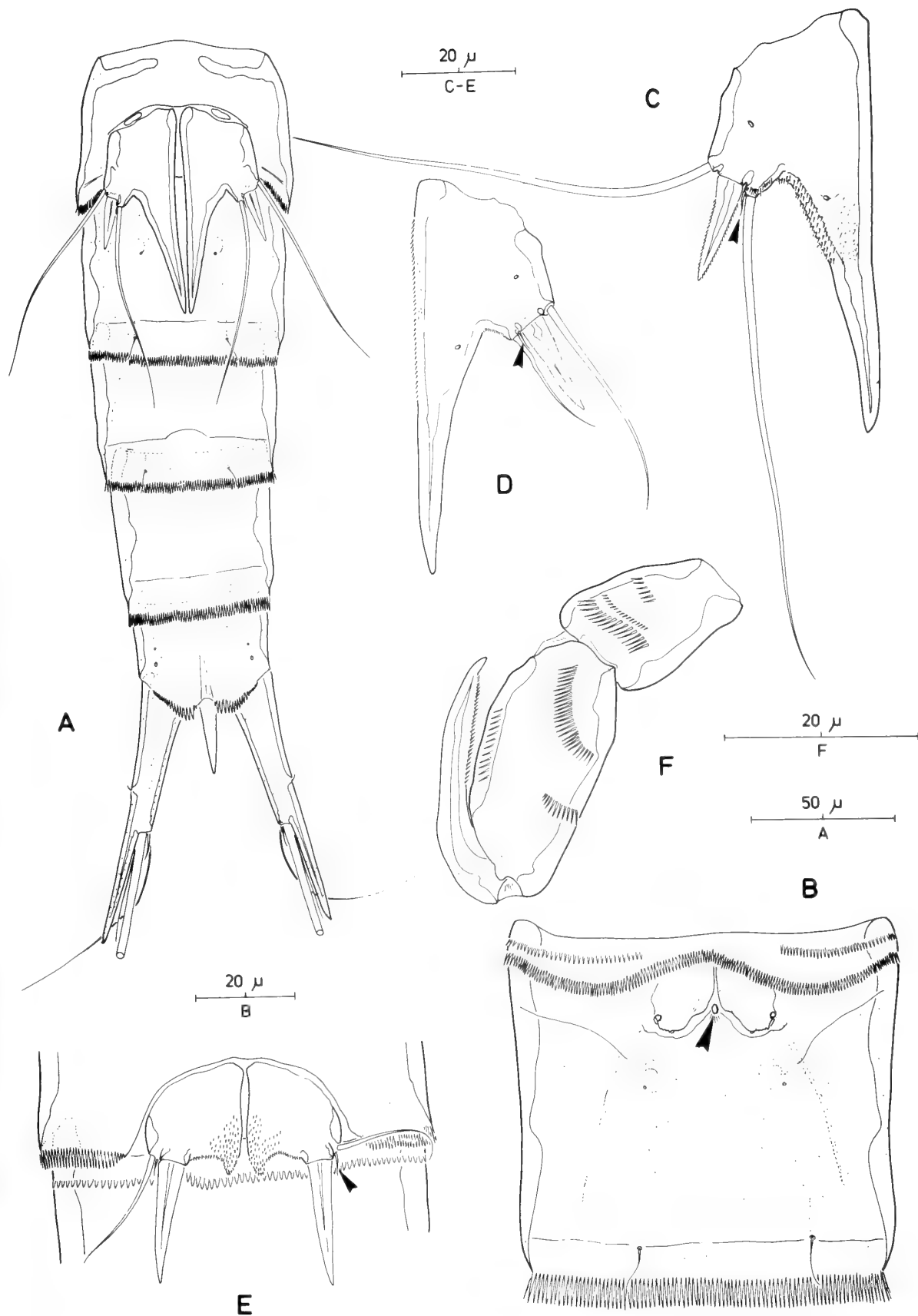


Fig. 3 *Syrticola intermedius* sp. nov. female. A, P1, anterior; B, P2, anterior; C, P3, anterior; D, P4, anterior.



g. 4 *Syrticola intermedius* sp. nov. female. A, Urosome, ventral; B, genital double-somite, ventral; C, P5, anterior. Male. D, P5, anterior; E, sixth pair of legs; F, maxilliped. [Arrows in C-E indicating vestigial seta; copulatory pore arrowed in B.]

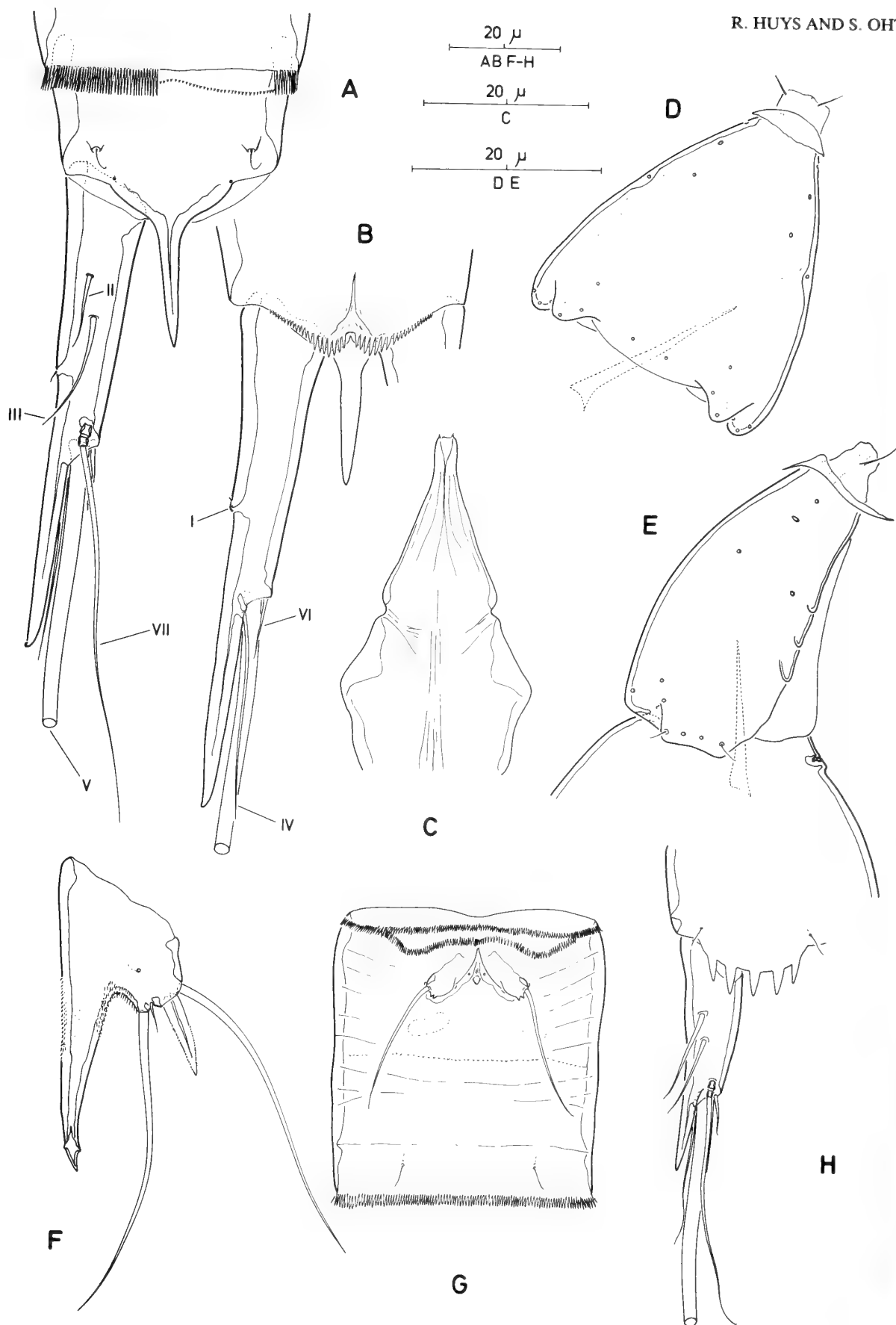


Fig. 5. *Syrticola intermedius* sp. nov. male. A, Anal somite and left caudal ramus, dorsal; B, anal somite and right caudal ramus, ventral; C, labrum, anterior. Female of undescribed tantulocaridan. D, Cephalic shield, dorsal; E, same, lateral. *Syrticola flandricus* female. F, P5, anterior; G, genital double-somite, ventral; H, anal operculum and left caudal ramus, dorsal.

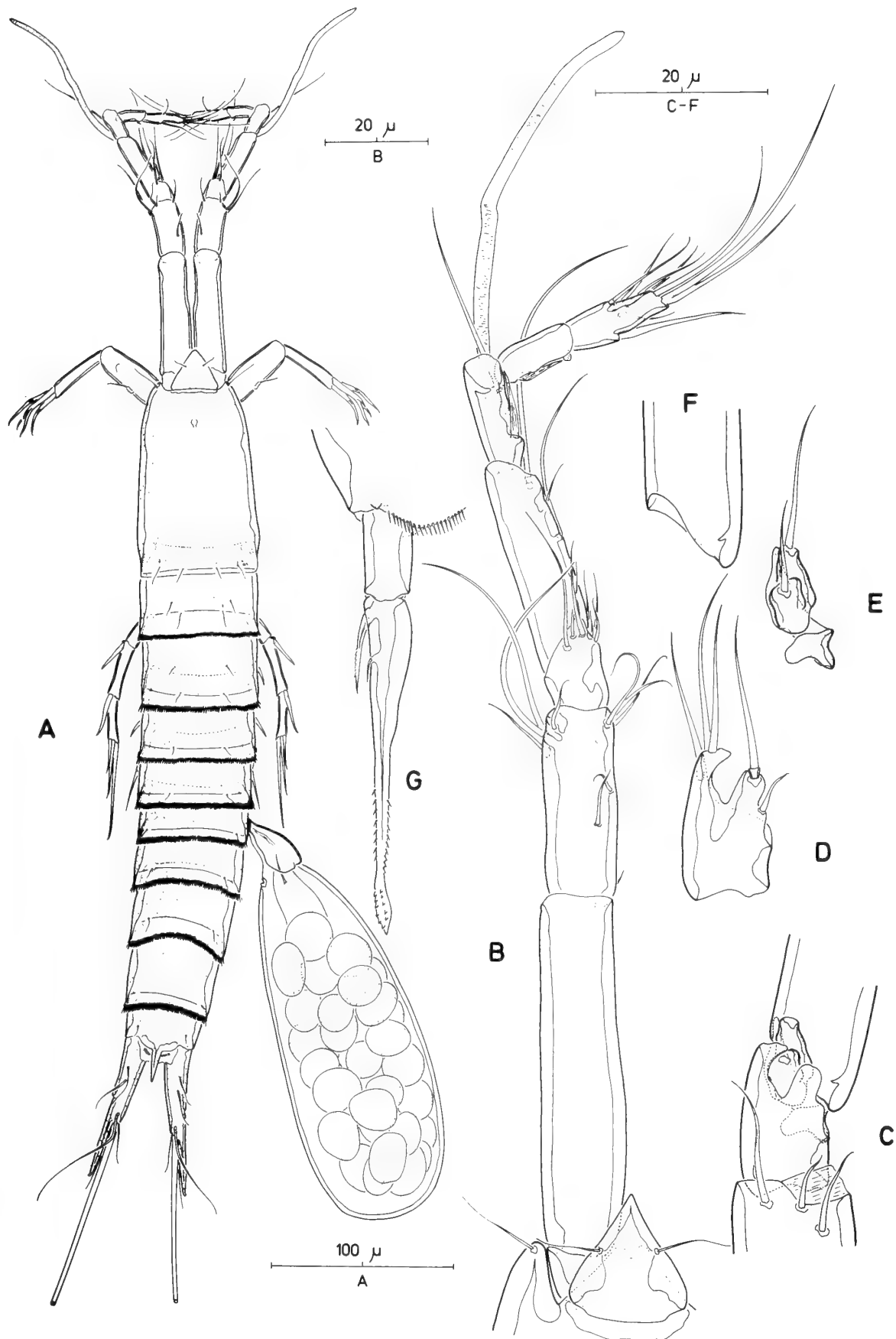


Fig. 6 *Syrticola intermedius* sp. nov. male. A, Habitus, dorsal; B, rostrum and antennule, dorsal; C, antennule, segments 3 and 4, anterior [armature of these segments omitted; segment 4 stippled]; D, antennular segment 3, anterior; E, antennular segment 4, anterior; F, proximal part of antennular segment 5, anterior; G, P3 endopod, anterior.

fine spinules. A distinct, ventrally directed, spinous process is located at the ventral midline between the maxillipedal syncoxae and the coxae of the first leg (Fig. 3A).

P2-P4 (Figs. 3B-D) with 3-segmented exopods and 1-segmented endopods. Intercoxal sclerites small, rectangular, bare (Fig. 3C). Spines of distal exopodal segment elongate and slender in P3 and P4. Inner seta of P2 endopod serrate and typically recurved (Fig. 3B). Inner margin of endopod P3 with serrate seta and vestigial seta represented by setule (see inset Fig. 3C). Distal spines of endopod pinnate in P2-P3, bare in P4. Armature formula as follows:

	coxa	basis	exopod segment 1 2 3	endopod segment 1 2
P1	0-0	1-1	I-0; I,2,0	0-1; 0,I,1
P2	0-0	1-0	I-0; I-0; I,II,0	0,II,1
P3	0-0	1-0	I-0; I-0; I,I,1	0,I,2
P4	0-0	1-0	I-0; I-0; I,I,1	0,I,1

Fifth legs (Figs. 4A, C) closely set together, no intercoxal sclerite. Baseoendopod and exopod fused to form a single plate with 2 secretory pores and 4 armature elements in total; endopodal lobe represented by long, triangular, spinous process without setae but with tiny spinules along proximal outer margin and on posterior surface; exopod presumably represented by weakly developed process bearing outer pinnate spine, inner slender seta and a vestigial seta in between. Outer basal seta elongate and bare.

MALE. Body length measured from tip of rostrum to posterior margin of caudal rami (Fig. 6A) 460 µm. Ornamentation of body somites generally as in female; genital and first abdominal somites separate, with spinulose hyaline frill each. Sexual dimorphism in antennule, P3 endopod, P5, P6 and in genital segmentation. Spermatophore not observed.

Antennule (Figs. 6B-F) indistinctly 8-segmented, articulating on a small pedestal. Relative lengths of first two segments as in female. Third and fourth segment (= ancestral segment XIII) interdigitating as shown in Fig. 6C. Major geniculation between segments 6 and 7. Segmental fusion pattern: I, II-VIII, IX-XII, XIII, XIV-XVIII, XIX-XX, XXI-XXII, XXIII-XVIII. Segment 6 with 1 modified flat spine and 1 setule, segment 7 with similar spine and 1 stubby pinnate element. Armature formula: [1, 9, 5, 2, 4+ae, 2, 2, 9].

P3 endopod (Fig. 6G) 2-segmented. Proximal segment unarmed. Distal segment drawn out into pinnate process (derived from distal spine in ♀) with spatulate tip bearing 2 rows of denticles; inner margin with short pinnate seta and minute setule.

P5 (Fig. 4D). Relative position, shape and armature largely similar to female except for the inner exopodal and outer basal seta being distinctly shorter. Ornamentation of endopodal lobe also slightly different with fewer spinules along the proximal outer margin and tiny spinules along the inner margin.

Sixth pair of legs (Fig. 4E) positioned midventrally, symmetrical; inner distal corner with numerous minute spinules and produced into a small process; armature consisting of inner strong spine, outer slender seta and a vestigial setule in between.

VARIABILITY. An aberrant left P3 was noticed in the holotype ♀ (Fig. 3C).

ETYMOLOGY. The species name is derived from the Latin *inter*, meaning between, and *medius*, meaning middle, and refers to the intermediate position between *S. galapagoensis* and the European species of the genus.

Syrticola flandricus Willems & Claeys, 1982 (Figs. 5F-H)

MATERIAL EXAMINED. 3 ♀♀ from off Walcheren, The Netherlands, southern North Sea, 51° 57'25" N, 02° 40'45" E, depth 44.5 m, coarse sandy sediment, 08 May 1991, coll. R. Huys. One ♀ in alcohol deposited under reg. no. 1992.1077.

The description given by Willems & Claeys (1982) is detailed and therefore only a few corrections to the original figures are noted here.

Antenna. The exopod possesses only one seta as in *S. intermedius* and *S. galapagoensis*. The oblique suture line has probably been mistaken for the lateral seta (compare Fig. 2D with Fig. 2B in Willems & Claeys (1982)), and it is conceivable that the same misinterpretation applies for *S. mediterraneus* (cf. Willems *et al.*, 1987: Fig. 3A).

Mandible. The basis bears only one seta; the supernumerary proximal 'setae' figured by Willems & Claeys are part of a transverse row of long spinules running around the lateral margin of the basis.

Maxillule. The arthrite of the praecoxa has 6 marginal and 2 surface setae, the coxal endite 2 setae and the distribution pattern of the palp setae is identical to *S. intermedius* (Fig. 2G).

Maxilliped. The endopodal claw bears an accessory setule at its base.

P1. A seta is located at the inner distal corner of the basis.

P5. The armature of the exopodal lobe consists of an outer spine, an inner seta and a setule in between (Fig. 5F).

The genital field is basically the same as in *S. intermedius* (Fig. 5G).

REMARKS

A single probably parthenogenetic female of a tantulocaridan was found attached to the pleurotergite of the P3-bearing somite of the holotype ♀ of *S. intermedius* (Fig. 1A). The specimen is about 160 µm long and is at an early stage of development. The larval postcephalic trunk had been sloughed already but no differentiating tissue could be observed inside the sac. The male paratype was also infested by a parthenogenetic female (Fig. 6A) which was larger (235 µm) and attached to the pleurotergite of the genital somite. Inside the sac a large number of small eggs of about 20-25 µm in diameter is contained. Both tantulocaridan stages most likely belong to an as yet undescribed species which was found to infest harpacticoids belonging to at least two other families (Huys *et al.*, in preparation). Since only the head shield (Figs. 5D-E) is left for comparison this identification has to be considered provisional.

DISCUSSION

Syrticola intermedius is the second species to be reported from the Indo-Pacific, the other species (under the name (?) *Notopontia galapagoensis*) being originally described from a sandy beach in the Galápagos (Mielke, 1982). Both species resemble each other morphologically. A comparison of the major diagnostic characters (Table 2) reveals two species groups in the genus *Syrticola*. The European group includes *S. trispinosus*, *S. flandricus* and *S. mediterraneus* and is characterized by a 6-segmented antennule (segments 6 and 7 fused) and the anal operculum possessing small spinous processes (Fig. 5H). The number of these projections ranges from (rarely) 0 to 5, though specimens with a single small process have not been recorded yet (Willems *et al.*, 1987). The second species group encompasses the two Indo-Pacific species which share a 7-segmented antennule and an operculum drawn out into a single median strong spike. Both species also share the plesiomorphic 2-segmented condition of the male P3 endopod, but the significance of this character is limited since not all the males are known in the European species group. The zoogeographical and morphological separation does not warrant the upgrading of these groupings to generic rank, however, since *S. intermedius* exhibits certain characters found in the European species. Outgroup comparison with *Notopontia* and *Leptopontia* suggests that the spiniform nature of the outer exopodal spine and the loss of the inner baseoendopodal seta are apomorphic character states for the fifth legs, linking the Japanese species with its European congeners. The outline of the anal operculum links *S. intermedius* to (?) *N. galapagoensis*, justifying the latter's re-allocation to *Syrticola* by Willems *et al.* (1987).

The possession of an aesthetasc-like structure on the syncoxa of the maxilla in *S. intermedius* is unusual. Re-examination of *S. flandricus* showed an unmodified seta in this position, in addition to the pinnate one also present in *S. intermedius*. Two setae are also reported on the syncoxal endite of *S. mediterraneus* and in the outgroup taxa *Notopontia* and *Leptopontia*. The report of 3 setae on this endite in *S. galapagoensis* (Mielke, 1982) therefore probably results from an misinterpretation of an aesthetasc-like structure. Without differential interference contrast microscopy the flaccid distal part is easily overlooked, thereby accentuating the lateral chitinized margins as setoid structures. The relative lengths of the enditic 'setae' in Mielke's (1982: Abb. 18E) illustration are suggestive of this interpretation.

The status of *S. trispinosus* remains enigmatic as ever. A.

Table 2 Comparison of *Syrticola* species.

	<i>trispinosus</i>	<i>flandricus</i>	<i>mediterraneus</i>	<i>galapagoensis</i>	<i>intermedius</i>
Antennule ♀	6-segmented	6-segmented	6-segmented	7-segmented	7-segmented
Inner seta P3 endopod ♀	?	present	absent	absent	present
Endopod P3 ♂	?	?	1-segmented	2-segmented	2-segmented
Outer element exopodal lobe P5 ♀♂	spiniform	spiniform	spiniform	setiform	spiniform
Inner seta endopodal lobe P5 ♀	absent	absent	absent	present	absent
Anal operculum processes	several, small	several, small	several, small	one, large	one, large
Body length ♀ (µm)	500	460-530	540-660	280-340	485
Body length ♂ (µm)	?	?	460-500	310-350	460
Distribution	Irish Sea	North Sea	Mediterranean	Galápagos	Japan

Scott's species is clearly closely related to *S. flandricus*. Willems & Claeys (1982) list a number of differences but except for the structure of the fifth leg, all of these can be attributed to deficiencies in the original decription. This, however, does not rule out *S. trispinosus* as a distinct species since the discovery of an as yet undescribed species of *Syrticola* in the North Sea has proven species discrimination in this genus to be rather unreliable. Pending re-examination of topotypes from the Isle of Man, *S. trispinosus* is relegated to *species inquirenda*.

KEY TO SPECIES

- 1. Antennule ♀ 7-segmented, anal operculum with one large, median spike 2.
Antennule ♀ 6-segmented, anal operculum with several small, spinous processes 3.
- 2. P3 endopod without inner seta; outer exopodal element P5 setiform *galapagoensis* (Mielke, 1982).
P3 endopod with inner seta; outer exopodal element P5 spiniform *intermedius* sp. nov.
- 3. P5 exopodal lobe with 2 spiniform elements
..... *trispinosus* (A. Scott, 1896).
Only one element of P5 exopodal lobe spiniform 4.
- 4. P3 endopod without inner seta
..... *mediterraneus* Willems *et al.*, 1987.
P3 endopod with inner seta
..... *flandricus* Willems & Claeys, 1982.

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- , — & Fiers, F. 1987. *Syrticola mediterraneus* n. sp., a harpacticoid copepod from the Bay of Calvi, Corsica. *Hydrobiologia* 153: 71-78.

Erratum

The following replaces Fig. 5, *Bull. Nat. Hist. Mus. (Zool.)* 58(1), p. 42.

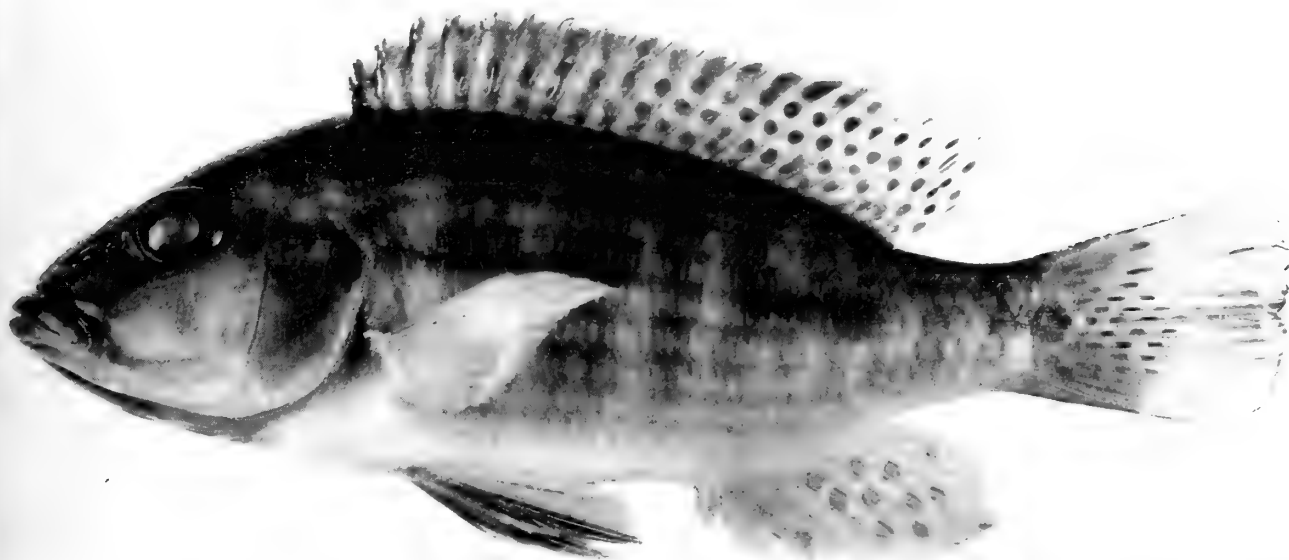


Fig. 5. *Pharyngochromis acuticeps* (Steind.) Adult male; S.L. 98.0 mm. Okavango system (RUSI 34974). Photographed by Paul Skelton and R. Stobbs.

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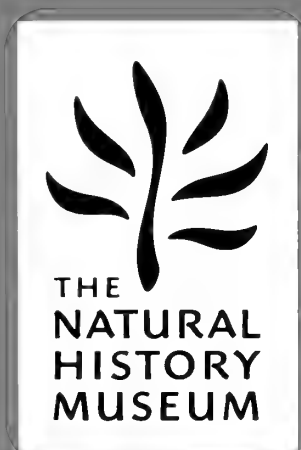
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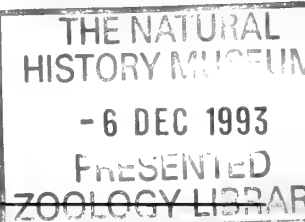
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The status of the Persian Gulf sea snake *Hydrophis lapemoides* (Gray, 1849) (Serpentes, Hydrophiidae)



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SYNOPSIS. A redescription is given of the two syntypes of *Hydrophis lapemoides* together with a description of specimens from the whole range of the species. Information on breeding and feeding biology and epizootic organisms of *H. lapemoides* is provided. Geographical variation was found between the following three areas: Andaman Sea and Malacca Strait, India and Sri Lanka, and Persian Gulf and Gulf of Oman. Finally the validity of *H. lapemoides* is tested against its congeners.

INTRODUCTION

In 1849, Gray described *Hydrophis lapemoides* on the basis of two specimens from Sri Lanka and Madras, respectively. In addition to the syntypes Smith (1926) had eight specimens available for characterizing the species. Smith recorded *H. lapemoides* from the Persian Gulf, and coasts of India and Ceylon, and considered it as a rare species. Volsøe (1939) collected eight specimens in the Persian Gulf and the Gulf of Oman, and concluded that *H. lapemoides* is a fairly common snake in these waters. Minton (1966) mentioned two specimens from the coast of Pakistan, and in 1981 Toriba & Sawai extended the known range of *H. lapemoides* from the East coast of India to Penang Island, Malaysia. Tamiya et al. (1983) identified some sea snakes from the Philippines as *H. lapemoides*, the identification, however, was questioned by Rasmussen (1987). Rasmussen recorded specimens from Singapore and Phuket Island, Thailand, thereby confirming the presence of *H. lapemoides* in the Malacca Strait and Andaman Sea, respectively. Recently Gasperetti (1988) considered *H. lapemoides* as the most frequent sea snake of the Persian Gulf.

On the basis of my own collections in 1985, 1987 and 1989 from Phuket Harbour, and in 1990 from Bahrain, Persian Gulf, I have a most welcome opportunity to describe *H. lapemoides* from its whole range, and to test the validity of *H. lapemoides* against its congeners. Some comments on the biology of *H. lapemoides* are also given.

MATERIALS AND METHODS

Material examined

Hydrophis lapemoides **BMNH**: 1946.1.7.2 (syntype) (formerly III.3.3.a) Ceylon. 1946.1.6.91 (syntype) (formerly III.3.3.b) Madras. 1946.1.3.88 (type of *H. stewartii*) (formerly 83.7.30.10) Orissa, Poorie. 1946.1.9.25 (type of *H. holdsworthii*) (formerly 72.1.26.41) Ceylon. 72.1.26.43 Ceylon. 80.11.10.199 Gwadur, Baluchistan. 1904.6.13.19 Mekran coast, Charbar. 1969.2902 Persian Gulf. 1972.689 Dubai, Trucial Oman. 1971.135-136 Bahrain. 1970.753 east coast of Bahrain. 1971.1461 Bahrain harbour. 1973.410 Sharjah, Trucial coast. 1983.1169 Najwa, Darninam reef. 1983.1163-1164 Dammam channel. 1983.1170 Oqair Bay. 1983.1172 Half Moon Bay, Saudi Arabia. 1985.646 Azaiba, Batinah. **FMNH**: 28310-11 Bahrain. 64432 Tarut Bay, Ras Tonura. 73996-97 Al Khobar, Arabia. 82577 Persian Gulf 26° 39'N, 50° 07'E. 121473 Ceylon. **USNM**: 127993 Ras Tanura, Saudi Arabia. 132402 Saudi Arabia. **RMNH**: 18026 Bahrain. **ZMUC**: R 66166-173 Persian Gulf (map in Volsøe, 1939). 66101 Malacca Str. (Singapore) 1° 35'N, 103° 01'E. R 66460, 66587-603, 66605-616, 66618-627, 66629-639 all collected from trawling boats in Phuket port, Phuket Island, west coast of peninsular Thailand. R 66927, 937, 939-941, 945, 950, 951, 954, 958, 961, 964, 965, 967, 968, 970, 971, 973-975, 980-1001, 1004-1006, 1009, 1011, 1013 Persian Gulf 100 km north-northeast of Bahrain.

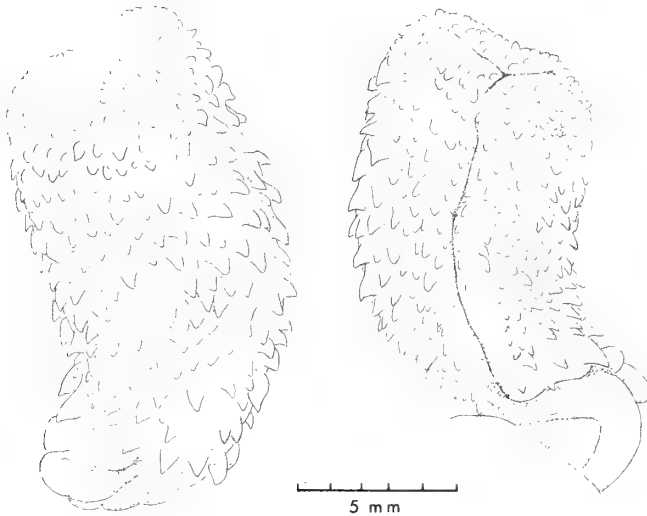


Fig. 1 Sulcate and asulcate side of everted hemipenis of *H. lapemoides* (ZMUC R 66620) from Phuket Harbour. Drawing by M. Andersen.

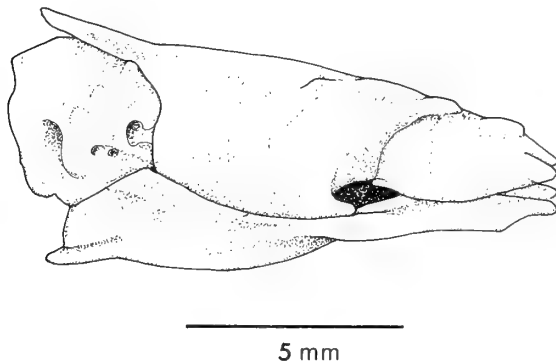


Fig. 2 Lateral aspect of anterior braincase of *H. lapemoides* in which the sphenoid is included in the margin of the anterior orifice of cavum epiptericum. Drawing by M. Andersen.

Methods

The measurements and counts follow Smith (1926) with some alterations as described below. For lateral head scales, both sides of the head have been examined and numbers are given separately. Number of maxillary teeth is given for the right side only.

Scale rows are counted directly around body (Thomas 1976). Minimum and maximum number of rows are given for comparison with the counts of Smith (1926, p.XVI).

Position of the tip of the heart and the anterior tip of the liver are determined in relation to the number of the adjacent ventral scales (VS). Relative position of the tip of the heart and the anterior part of the liver is expressed as the percentage of the total number of ventral scales (% VS). Vertebral counts are obtained from soft radiographs. Three counts are obtained from each snake: number of body vertebrae (VB-body), number of tail vertebrae (VB-tail), and number of vertebrae from the head to the tip of the heart (VB-heart). Body and tail are separated by the presence of the first pair of forked ribs in the cloacal region; this pair of ribs is included in the number of tail vertebrae. Tip of the heart was indicated in

the x-ray radiographs by inserting a needle perpendicular to the long axis of the body pointing at the vertebrae opposite the tip of the heart. Relative position of the tip of the heart is expressed as the percentage of the total number of body vertebrae (% VB). Terms and description of the hemipenis follow Dowling & Savage (1960). Hemipenis was described in everted condition. All measurements are given to the nearest centimeter. Meristic and mensural data given as $x \pm SD$.

In the following description of the two syntypes *H. lapemoides* III.3.3.a, a subadult female (syntype a) is given first, and III.3.3.b, a juvenile male (syntype b) is given when different from type a. The description of the examined specimens is given in parentheses when different from the types.

The following are abbreviations (Leviton et al., 1985) used for the collections: BMNH: The Natural History Museum, London; FMNH: Field Museum of Natural History, Chicago; RMNH: Rijksmuseum van Natuurlijke Historie, Leiden; USNM: National Museum of Natural History, Smithsonian, Washington; ZMUC: Zoological Museum, University of Copenhagen.

SYSTEMATIC ACCOUNT

Hydrophis lapemoides (Gray, 1849).

Aturia lapemoides Gray, 1849:46.

Hydrophis holdsworthii Günther, 1872:33.

Hydrophis stewartii Anderson, 1872:399.

Distira lapemoides, Wall, 1909:227.

Hydrophis lapemoides, Smith, 1926:86, 1943:461. Volsøe, 1939:19. Minton, 1966:146. McDowell, 1972:229. Voris, 1977:91. De Silva, 1980:399. Toriba & Sawai, 1981:134. Rasmussen 1987:57, 1989:413, 1992:92. Gasperetti, 1988:312. Bussarawit et al. 1989:222. McCarthy & Warrell, 1991:163.

Diagnosis

Eight to 13 maxillary teeth behind poison fang, 28–35 scale rows on neck, 40–57 scale rows on body. Number of ventral scales 288–395, tip of heart extending to ventral number 106–155. Number of body vertebrae 164–188, tip of heart extending to vertebrae number 73–94. Head dark dorsally with curved white mark, disappearing with age. Body with black bands forming rhombic spots dorsally and disappearing with age ventrally. Tail with black bands, disappearing with age, posterior part normally black.

Description of the syntypes and the examined specimens

EXTERNAL MORPHOLOGICAL CHARACTERS. Maxillary teeth behind poison-fang 10. Dentary teeth, pterygoid teeth and palatine teeth not counted on syntypes; for the examined specimens see Table 1. One pre- and two postoculars on both sides (one pre- and two or three postoculars). Three anterior temporals on both sides (two or three). Eight supralabials on both sides (7–10 in males, 7–10 in females). First and second supralabials in contact with nasal, second and third in contact with preocular, third and fourth in contact with eye, syntype b; only third in contact with eye, fourth is divided horizontally. Eight infralabials on both sides, first, second and third on each side in contact with anterior pair of sublinguals,



Fig. 3 Habitus of the juvenile type specimen of *H. lapemoides* (BMNH 1946.1.6.91) from Madras, India. Photo by G. Brovad.

which are well developed and in contact with one another; third and fourth infralabials touching posterior pair of sublinguals, which are well developed and separated from one another posteriorly. A series of small cuneated scales at the oral margin after the third infralabial, syntype b; second infralabial. Scale rows on neck 29, syntype b; 32 (28-34 in males, 28-35 in females), on body 45, syntype b; 51 (40-51 in males, 41-57 in females). Ventrals 349, syntype b; 318 (288-365 in males, 293-395 in females), distinct throughout, bicarinate, about twice as broad as adjacent scales anteriorly, narrower posteriorly. Subcaudals 44, syntype b; 49 (37-56 in males, 36-53 in females).

INTERNAL MORPHOLOGICAL CHARACTERS. Tip of heart extending to ventral scale number 127, syntype b; 119 (106-141 in males, 106-155 in females), %VS heart 36.38%, syntype b; 37.42% (34.2-41.5 in males, 33.8-40.9 in females). Anterior end of liver situated at ventral scale number 133, syntype b; 120 (110-144 in males, 107-157 in females), %VS liver 38.10%, syntype b; 37.74% (34.4-41.5% in males, 34.4-41.2%). In type a, a small interval separates the heart and the liver. Number of body vertebrae 171, syntype b; 165 (164-188 in males, 171-186 in females). Number of tail

vertebrae 33, syntype b; 30 (31-40 in males, 28-38 in females). Tip of heart extending to vertebrae number 81, syntype b; 82 (73-90 in males, 79-94 in females), %VB heart 47.36%, in syntype b; 49.70% (43.5-51.1% in males, 45.1-51.7% in females).

HEMIPENIS. Hemipenis feebly bilobed with a bifurcate sulcus spermaticus (Fig. 1). Bifurcation near apical end of organ (Fig. 1). Organ covered with spines gradually decreasing in size and becoming more scattered at the distal end. A finger-like fold at the proximal portion opposite the sulcus spermaticus.

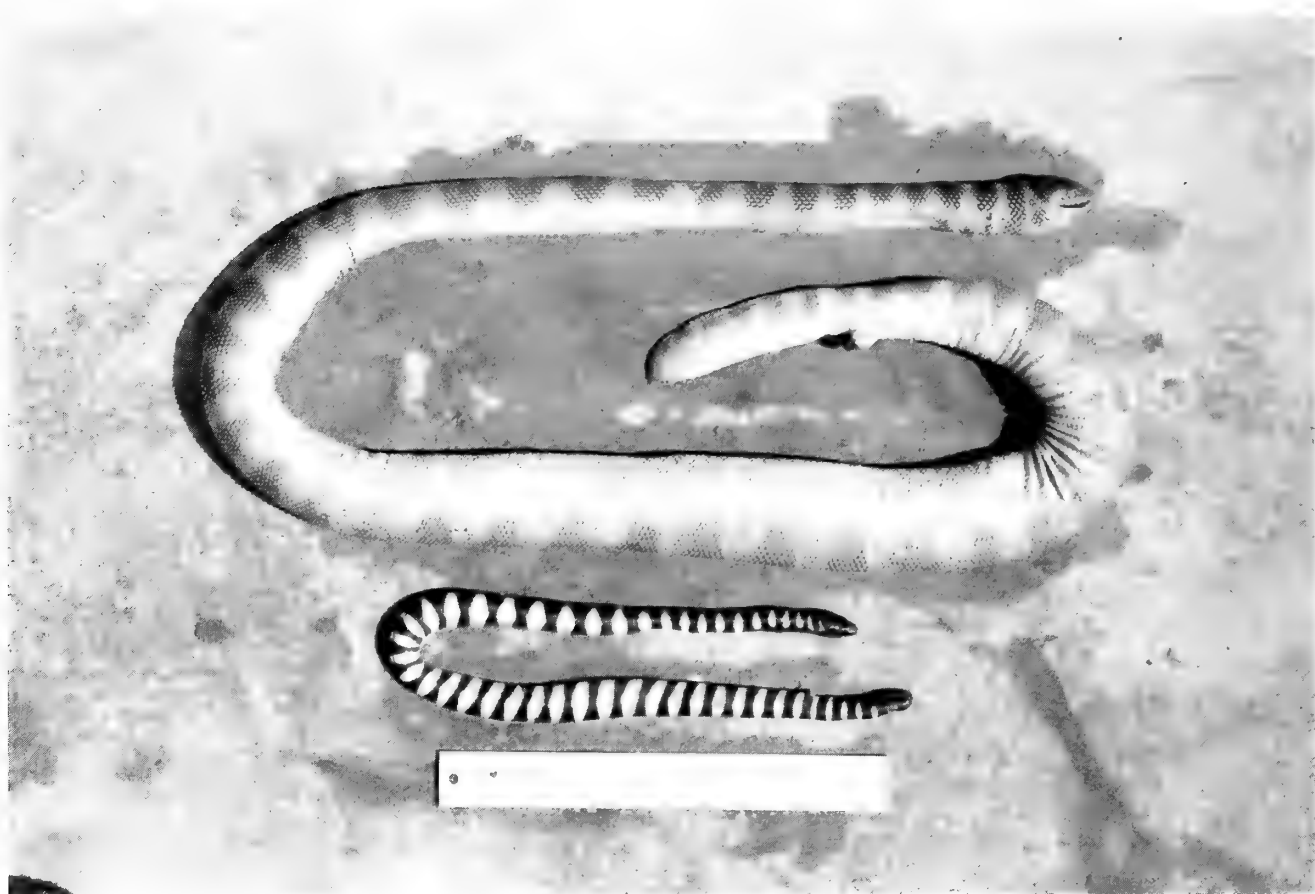
SKULL MORPHOLOGY (based on skulls from the Persian Gulf and Andaman sea (Phuket)). Posterior half of parietal with a distinct ridge being about 1/3 of the total length (midline). Supratemporals (squamosals) reach parietal, and extend as far posteriorly as posterior part of exoccipitals. Postorbital bones barely touch frontals. Ventral extensions of frontals do not overhang trabecular grooves. Sphenoid enters broadly into margin of anterior orifice of cavum epiptericum (Fig. 2). Sphenoid with low but distinct keel. Both anterior and posterior Vidian foramen on the ventral side of sphenoid, and

Table 1 Geographic variation in number of the teeth on maxilla, palatine, pterygoid and dentary bone.

	<i>n</i>	Maxillary teeth	<i>n</i>	Palatine teeth	Pterygoid teeth	Dentary teeth
Andaman Sea Malacca Str.	53	10–13	20	8–10	23–30	20–23
India Sri Lanka	5	9–10	–	–	–	–
Persian Gulf Gulf of Oman	73	8–11	12	7–10	21–26	20–21

going back, yellowish ventrally, some older specimens without a curved mark. Body with black bands (29–52) forming rhombic spots dorsally and disappearing with age ventrally (Figs. 4 and 5). Tail with black bands (5–8), disappearing with age, posterior part black (Fig. 4).

BREEDING BIOLOGY. Six of 17 females (collected in September–November 1987) from Phuket were pregnant. Three specimens contained 2 full-term embryos each, two specimens contained 4 full-term embryos each, and one specimen contained 1 full-term embryo. Pregnant females were collected in the period 3rd October to 4th November. None of the females collected in February–March 1989 were pregnant. The smallest embryo measured 9 cm (3rd October)

**Fig. 4** Habitus of a juvenile and an adult *H. lapemoides* (ZMUC R 66992, 66993) from the Persian Gulf. Photo by M. Andersen.

in respect of the length of the Vidian canals they are symmetric. Palatine exceeding maxilla in forward extension, and without a flange for the anterior medial process of maxilla. Palatine-ptyergoid articulation anterior to maxilla-ectopterygoid articulation. Fangs separated from solid maxillary teeth by a diastema. Maxillary bone slightly longer than ectopterygoid. Solid maxillary teeth shorter than fangs. For number of teeth on maxilla, palatine, pterygoid, and dentary bones see Table 1.

COLOUR. Juveniles: Head black with a yellowish curved mark above, body yellowish or whitish, encircled by black bands broadest dorsally (Figs. 3 and 4). Adults: Head dark dorsally with curved white mark above, starting forehead

and the largest 26 cm (19th October). The female collected 4th November had embryos measuring 22 cm. Thus *H. lapemoides* seems to be a k-strategist (Lemen & Voris, 1981) producing small clutches of relatively large offspring.

None of the females examined from the Persian Gulf were pregnant, however, Volsøe (1939) mentioned three females with eggs, and again the clutch size was very small (two females with 2 eggs, one female with 3 eggs). Only two of the three specimens have a collection date, and both were from April (Volsøe, 1939).

FEEDING BIOLOGY. Remains of the following four fish families were identified in stomach contents from *H. lapemoides* collected at Phuket harbour; Gobiidae, Labridae, Mullidae,



Fig. 5 Habitus of the subadult type specimen of *H. lapemoides* (BMNH 1946.1.7.2) from Sri Lanka. Photo by G. Brovad.

and Pseudochromidae. Pseudochromidae was found as prey in a sea snake stomach for the first time, and Labridae and Mullidae are new prey records for *H. lapemoides* (Voris & Voris, 1983). The stomach contents from *H. lapemoides* collected in Bahrain were too digested to be identified, however, Volsøe (1939) mentioned Gobiidae in stomachs of 5 specimens of *H. lapemoides* from the Persian Gulf. Furthermore Voris & Voris (1983) mentioned Anguilliformes and Ophiichthidae as stomach contents from *H. lapemoides*.

EPIZOOIC ORGANISMS. Five of the 51 specimens examined from the Andaman Sea and Malacca Strait had between one and five barnacles (*Platylepas ophiophilus*) on the skin. Two of the seven specimens from India and Sri Lanka had three and 20 *P. ophiophilus* on the skin, respectively. 25 of the 71 specimens from the Persian Gulf and the Gulf of Oman had between one and 181 *P. ophiophilus* on the skin. Most of the barnacles were on the posterior part of the body. *P. ophiophilus* is found only on sea snakes (Zann et al., 1975), and has been found on many species (Rasmussen, 1992; Zann, 1975).

DISTRIBUTION. *H. lapemoides* is found from the Persian Gulf in west, to the Malacca Strait (Singapore) in east. Specimens have been collected from the Persian Gulf, the Gulf of Oman, the coast of Pakistan, India, and Sri Lanka, the west coast of peninsular Thailand, Penang (Malaysia), and Singapore. (Ahmed, 1975; Bussarawit et al., 1989; Gasperetti,

1988; McCarthy & Warrell, 1991; Minton, 1966; Rasmussen, 1987; Smith, 1926, 1943; Toriba & Sawai, 1981; Volsøe, 1939;).

RECENT COLLECTION DATA. *H. lapemoides* was collected in different periods of 1985, 1987, and 1989 from fishing boats in Phuket harbour, Phuket Island, on the west coast of peninsular Thailand. The most common sea snake brought to the harbour by fishing boats was *Lapemis hardwickii* (over 80% of all sea snakes caught by trawl) followed by *H. ornatus*, and then *H. lapemoides*. According to the fishermen, the sea snakes were caught mainly by sea-going trawler-boats, fishing in waters more than 10 m deep. No further information was available, as the fishermen were rather secretive about the exact position of their fishing grounds. During collection in the Persian Gulf (Bahrain) in February 1990, we went to an area about 100 km north-northeast of Bahrain, on board a trawling boat. On a 3 days trip we collected 7 specimens of *H. lapemoides*, 2 specimens of *Thalassophina viperina*, and 1 specimen of *H. ornatus*. They were all caught by trawl in a depth of 27-30 m, the bottom material was gravel. We also collected sea snakes at Bahrain harbour from 6 trawling boats, all working in the same area as mentioned above. In a period of 10 days (each boat was out 3 to 4 times in that period), a total of 110 sea snakes was collected, and 96% of the snakes were identified as *H. lapemoides*.

SPECIES ASSIGNMENT. The material examined is separated into three geographical regions: Andaman Sea and Malacca Strait, India and Sri Lanka, and Persian Gulf and Gulf of Oman (Tables 2 and 3, Figs. 6 and 7). When comparing specimens from the three areas mentioned above, geographical variation is found in general body form (specimens from the Persian Gulf look more robust than specimens from Andaman Sea and Malacca Strait), in scale rows on neck in relation to scale rows on body (Fig. 6), in number of vertebrae (Table 3), and in number of vertebrae in relation to VB heart (Table 3, Fig. 7). However, it is difficult to decide whether the variation indicates a cline or distinct geographic forms, as material is still missing from Bangladesh and Burma, and so are representative samples from Pakistan, India, and Sri Lanka.

Both Boulenger (1896), Wall (1909) and Smith (1926) referred the type specimen described by Anderson in 1872 under the name *H. stewartii* to *H. lapemoides*. Having examined the specimen, I have serious doubt about its assignment. 52 Scale rows on body in relation to 30 scale rows on neck (Fig. 6), and 182 vertebrae in relation to 94 VB heart (Fig. 7) indicate that the specimen belongs to a distinct taxon. But as representative material is lacking from India and Sri Lanka, I tentatively assign it to *H. lapemoides*. Further material may show whether it is a valid taxon.

Dunson & Minton (1978) caught some sea snakes in the Philippines, during the Visayan Sea Expedition of R/V Alpha Helix, and identified them as *H. ornatus*. In 1983 Tamiya et al. reclassified the specimens as *H. lapemoides*, and later Rasmussen (1989) reexamined the specimens and identified them as *H. lamberti*. Comparison of the above mentioned specimens with *H. lapemoides* from Andaman Sea and Malacca Strait, shows that they differ in following characters: Scale rows on neck (*H. lamberti*, 37-45), VS heart tip (*H. lamberti*, 87-109), and VS liver (*H. lamberti*, 86-108), VB heart tip (*H. lamberti*, 65-71), and color pattern (Rasmussen, 1989). Comparing the skull, *H. lamberti* shows a more robust parietal, with a longer ridge (from 1/2 to 2/3 of the total length of parietal bone in midline), and with a less globular form than *H. lapemoides*. A single specimen of *H. lamberti* (FMNH 313058) was collected sympatrically with *H. lapemoides* (ZMUC 66101) in the area of Singapore, and also here the two species are distinct on the characters mentioned above.

McCarthy & Warrell (1991) referred to a specimen (BMNH 1987.172) from the Gulf of Siam (Samut Sakhon) as '*H. sp. near H. lapemoides*'. I have examined this specimen and agree that it is very similar to *H. lapemoides*, however, it differs in number of scale rows around body in relation to scale rows on neck (Fig. 6) and in number of vertebrae in relation to VB heart (Fig. 7). Compared to *H. lapemoides* from Malacca Strait and Andaman Sea it is very long (1.1 m) and very robust in body and head form. In general shape it is much closer to *H. ornatus* and *H. lamberti*, although the characters differ here, too. Accordingly I think '*H. sp. near H. lapemoides*' should be separated from *H. lapemoides*, but further studies are needed to find out whether the specimen belongs to some of the more robust species in the Gulf of Siam or is an unknown species.

Generic assignment

H. lapemoides has a combination of characters which places it in the genus *Hydrophis* as defined by Smith (1926): maxillary bone not extending forward beyond the palatine; poison-fang followed, after a diastema, by from 1 to 18 teeth; palatine straight; nostrils superior; nasal shields in contact with one another; head shields large, regular; and ventrals small, distinct throughout and normally entire.

McDOWELL'S SUBGENERIC ASSIGNMENT. In 1972 McDowell recognized three subgenera in the genus *Hydrophis*, however, making a cladistic analysis (Rasmussen, in press) of the subgenus *Chitulia* (formerly *Aturia*, see Williams & Wallach, 1989), the results indicated that the group was paraphyletic, held together by plesiomorphic character states. Nevertheless, many of McDowell's character states are most useful in making a congeneric comparison.

Comparison with sympatric species

In the genus *Hydrophis* the following species are sympatric with *H. lapemoides*: *H. bituberculatus*, *H. brookii*, *H. caeruleus*, *H. cantoris*, *H. cyanocinctus*, *H. fasciatus*, *H. gracilis*, *H. inornatus*, *H. klossi*, *H. lamberti*, *H. mamillaris*, *H. melanosoma*, *H. obscurus*, *H. ornatus*, *H. spiralis*, *H. stricticollis*, and *H. torquatus*. (Bussarawit et al., 1989; De Silva, 1980; Gasperetti, 1988; McCarthy & Warrell, 1991; Minton, 1966; Murthy,

Table 2 Geographic variation of external and internal characters in *H. lapemoides*.

	Sex	n	Ventrals	VS-heart	% VS-heart	VS-liver	% VS-liver
Andaman Sea and Malacca Str.	M	28	288-347	106-131	34.2-40.6	110-133	35.7-41.3
		$\bar{x} \pm \text{SD}$	317 \pm 13	118 \pm 6.7	37.5 \pm 1.4	120 \pm 6.2	38.1 \pm 1.3
	F	23	299-378	106-140	33.8-38.5	107-143	34.4-39.1
		$\bar{x} \pm \text{SD}$	341 \pm 20	122 \pm 7.7	35.7 \pm 1.2	124 \pm 7.7	36.3 \pm 1.2
India and Sri Lanka	M	2	313-318	114-119	36.4-37.4	114-120	34.4-37.7
		$\bar{x} \pm \text{SD}$	315 \pm 3.5	116 \pm 35	36.9 \pm 0.7	117 \pm 4.2	37.1 \pm 0.9
	F	5	313-376	117-145	35.1-39.0	117-146	35.1-39.3
		$\bar{x} \pm \text{SD}$	347 \pm 24	127 \pm 12	37.3 \pm 1.8	129 \pm 13	37.8 \pm 1.8
Persian Gulf and Gulf of Oman	M	45	293-369	111-141	35.0-41.5	113-144	36.3-41.5
		$\bar{x} \pm \text{SD}$	320 \pm 16	123 \pm 7.2	38.5 \pm 1.4	124 \pm 7.1	38.8 \pm 1.4
	F	25	300-395	114-155	34.6-40.9	114-157	34.6-41.2
		$\bar{x} \pm \text{SD}$	347 \pm 23	129 \pm 10	37.5 \pm 1.6	130 \pm 10	37.7 \pm 1.6

VS-heart, VS-liver = position of tip of the heart and anterior tip of liver in relation to the number of the adjacent ventral scales, respectively. %VS-heart, %VS-liver = relative position of tip of the heart and anterior tip of the liver in number of ventral scales, expressed as percentage of total number of ventral scales.

Table 3 Geographic variation of internal characters in *H. lapemoides*.

	Sex	<i>n</i>	VB-body	VB-heart	%VB-heart	VB-tail
Andaman Sea and Malacca Str.	M	28 <i>x</i> ±SD	164–174 170±2.7	73–83 79±2.3	43.5–48.0 46.7±1.1	31–38 34±2.0
	F	23 <i>x</i> ±SD	171–180 174±2.5	79–86 82±1.8	45.1–49.1 47.0±1.1	28–38 31±2.5
India and Sri Lanka	M	2 <i>x</i> ±SD	165–174 169±6.4	79–82 80±2.1	45.4–49.7 47.5±3.0	37(<i>n</i> =1)
	F	5 <i>x</i> ±SD	171–182 176±4.9	81–94 85±5.1	45.8–51.7 48.5±2.3	30–35 33±1.9
Persian Gulf and Oman	M	45 ±SD	171–188 177±3.3	79–90 85±2.3	45.6–51.1 47.9±1.3	33–40 37±1.7
	F	26 <i>x</i> ±SD	172–186 181±3.6	81–90 86±2.4	46.6–49.2 48.0±0.8	30–36 34±1.7

VB-body = number of body vertebrae. VB-heart = position of the tip of the heart in relation to the number of vertebrae. %VB-heart = relative position of tip of the heart in number of vertebrae, expressed as percentage of total number of vertebrae. VB-tail = number of tail vertebrae.

1985; Rasmussen, 1987, 1989, 1992; Smith, 1926, 1930, 1943; Taylor, 1965; Toriba & Sawai, 1981; Tweedie, 1983).

The sympatric species differ from *H. lapemoides* in the following characters: *H. cyanocinctus* and *H. spiralis* have the sphenoid nearly excluded from the ventral margin of the optic fenestra (McDowell, 1972; Rasmussen, 1992: Fig. 5), a lesser number (< 9) of maxillary teeth, (< 20) pterygoid teeth, and (< 20) dentary teeth, and a different colour pattern (Bussarawit et al., 1989; McDowell, 1972; Rasmussen, in press; Smith, 1926). *H. brookii*, *H. cantoris*, *H. fasciatus*, *H. gracilis*, *H. klossi*, *H. melanostoma*, and *H. obscurus* have a triangular flange on the palatine (McDowell, 1972; Rasmussen, 1992: Fig. 4), and a lesser number (< 8) of maxillary teeth, (< 17) pterygoid teeth, and (< 16) dentary teeth (McDowell, 1972). *H. bituberculatus* has a lesser number (25–29) of scale rows around neck, a lesser number (247–290) of ventrals, a lower position (90–105 VS) of heart tip, and a different colour pattern (Rasmussen, 1992). *H. caeruleus* has a higher number (14–18) of maxillary teeth (Smith, 1926), a higher position (96–99 VB, based on 3 specimens from Phuket harbour) of heart tip, and a different colour pattern (Bussarawit et al., 1989; Smith, 1926; Tweedie, 1983). *H. inornatus* (type specimen BMNH 1946.1.1.27 formerly III.7.1.a.) has a lesser number (253) of ventrals, a lower position (86 VS) of heart tip, a lower position (67 VB) of heart tip, and a different colour pattern (Rasmussen, 1989). *H. lamberti* is compared with *H. lapemoides* in the section concerning species assignment. *H. mamillaris* has a smaller head, a lesser number (25–29, 35–43) of scale rows on neck and body, and a different colour pattern (Minton, 1966; Smith, 1943). *H. ornatus* has a lesser number (224–294) of ventrals, a lower position (72–104 VS) of heart tip, a lower position (59–65 VB) of heart tip, and a different colour pattern (Rasmussen, 1989). *H. striticollis* has a smaller head, a higher number (> 200 VB, Voris, 1975, and own observation) of vertebrae, and the hemipenis is bilobed half way down. *H. torquatus* has a higher position (91–105 VB) of heart tip, and a lesser number (7–8) of maxillary teeth (only in Malacca strait) (own observation).

Comparison with allopatric species

In the genus *Hydrophis* the following species are allopatric with *H. lapemoides*: *H. belcheri*, *H. coggeri*, *H. czeblukovi*,

H. elegans, *H. geometricus*, *H. macdowellii*, *H. melanocephalus*, *H. pacificus*, *H. parviceps*, and *H. vorisi*. (Bussarawit et al., 1989; Cogger, 1975; Kharin, 1983, 1984a, 1984b; McCarthy & Warrell, 1991; Smith, 1986; Smith, 1926, 1930, 1935). The allopatric species differ from *H. lapemoides* in the following characters: *H. coggeri*, *H. czeblukovi*, *H. elegans*, *H. melanocephalus*, and *H. pacificus* have the sphenoid nearly excluded from the ventral margin of the optic fenestra (Kharin, 1984b; McDowell, 1972; Rasmussen, 1992: Fig. 5) and a lesser number (< 9) of maxillary teeth, (< 20) pterygoid teeth, and (< 20) dentary teeth (Kharin, 1984b; McDowell, 1972). *H. parviceps* and *H. vorisi* have a triangular flange on the palatine (Kharin, 1984a; McDowell, 1972; Rasmussen, 1992: Fig. 4), and a lesser number (< 8) of maxillary teeth, (< 17) pterygoid teeth, and (< 17) dentary teeth (Kharin, 1984a; McDowell, 1972; Smith, 1935). *H. belcheri* has a lesser number (24–26, 32–36) of scale rows on neck and body, a lesser number (14–17) of pterygoid teeth, and no cuneate scales at infralabials (McCarthy & Warrell, 1991). *H. geometricus* has a high number (51–58, a small overlap) of scale rows on body, and a different colour pattern (Smith, 1986: Fig. 1). *H. macdowellii* has a lesser number (< 8) of maxillary teeth, (< 16) pterygoid teeth, and (< 17) dentary teeth, and a lesser number (256–266) of ventrals (Kharin, 1983).

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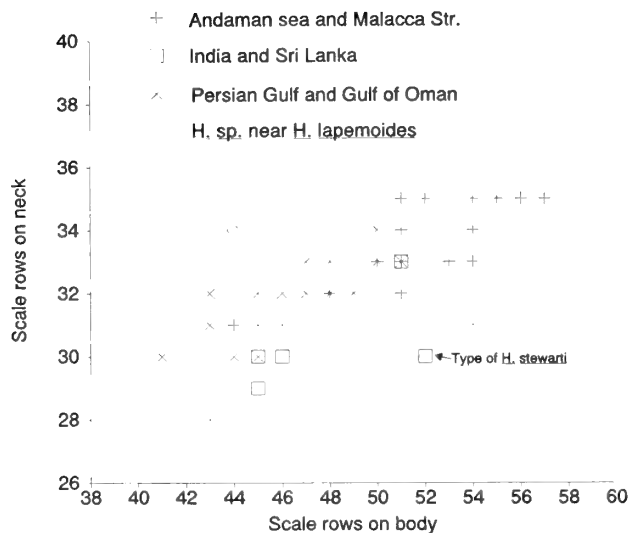
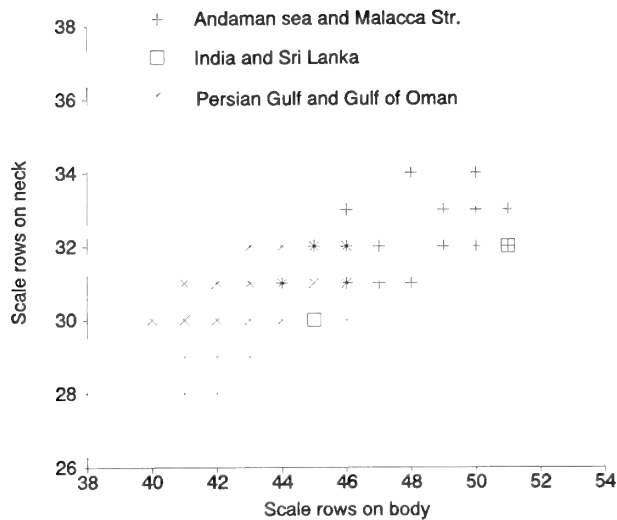


Fig. 6 Relation between number of scale rows on body and number of scale rows on neck in males (top) and females (bottom) of *H. lapemoides*, showing geographic variation.

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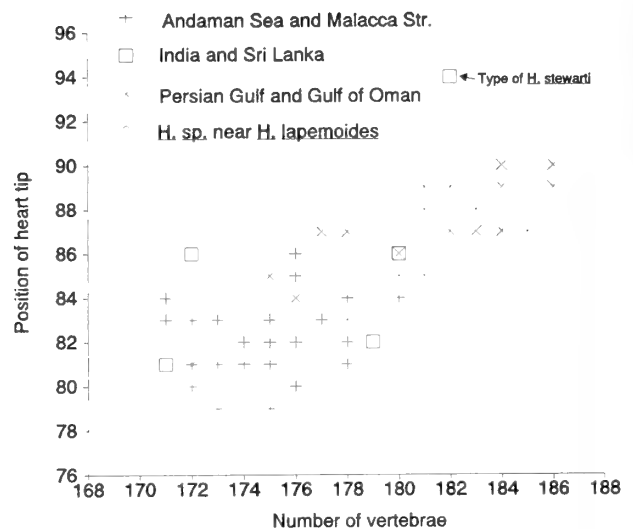
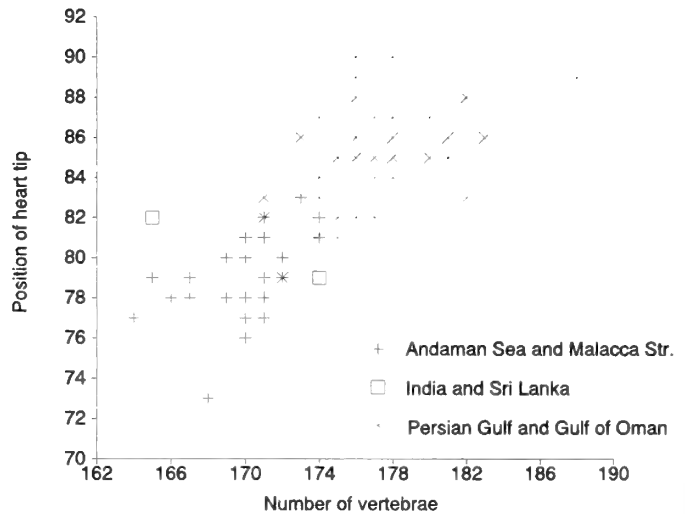


Fig. 7 Relation between number of body vertebrae and position of heart tip in males (top) and females (bottom) of *H. lapemoides*, showing geographic variation.

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Taxonomic revision of some Recent agglutinated foraminifera from the Malay Archipelago, in the Millett Collection, The Natural History Museum, London

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SYNOPSIS. Eleven species of Recent agglutinated foraminifera in the Millett Collection from the Malay Archipelago, have been re-examined and revised systematically. They were originally described and illustrated in 1899 and 1900 with excellent lithographic drawings in the hand of Millett. With rare exceptions, the actual figured specimens, though not marked as such, have been recognised in his Collection. The species are here redescribed, re-illustrated by SEM photography and, where necessary, supplemented by new data, notably from similar environments in Brazil. All, with the exception of *Paratrochammina simplissima* (Cushman & McCulloch) and possibly *Trochammina? milleti* sp.nov., are brackish-water forms.

New taxa are *Trunculocavus durrandi* gen. et sp.nov. and *Trochammina? milleti* sp.nov. A lectotype is designated for *Acupeina triperforata* (Millett), while *Ammobaculites salsus* var. *distinctus* Cushman & Brönnimann is elevated to specific rank and placed in *Ammotium*. All the species reviewed in this paper belong to the Suborder Trochamminina.

INTRODUCTION

Durrand (1898) gives what locality information there is about the Malay samples from which Fortescue William Millett made his classic study of the foraminifera. Durrand had for several years, out of his own interest, obtained small samples from around the SW Pacific and had examined them for the microscopical fauna and flora. In 1889 he had succeeded in getting the Netherlands India Steam Navigation Company (then controlled by the British India Steam Navigation Company) . . . 'to instruct the commanders of their fleet plying about the islands of the Archipelago, to collect bottom from each port of call'. The 'cleaned material' was picked over first by Durrand and then the foraminifera were determined by Millett and published (1898–1904) in 17 parts in the *Journal of the Royal Microscopical Society*. In all, 468 species and varieties were listed by Millett, 45 of them new. The descriptions were accompanied by 19 plates of quite exceptional and accurate drawings, from Millett's own hand.

The samples came from anchor mud where the ships were moored, more or less close inshore . . . 'in about 12 or 14 fathoms' (22–25 m). Unfortunately, a number of labels on the flasks of sediment became illegible through getting soaked by leakage, so the locality information is somewhat sketchy. The original samples each contained about 4 lbs (1.8 kg) of solid matter.

The material came from two areas. Area 1 ('from Celebes in the north and west, to Java in the south and New Guinea,

Aru, and the Islands in the east, including such stations as Banda, Amboina, Flores, Sumbawa and Timor') contains stations 1–16; area 2 ('Singapore in the north, Banka in the south, Sumatra in the west, and Borneo in the east') contains stations 17–31.

As part of a major revision of shallow-water agglutinating foraminifera of the Indo-Pacific region (see also Brönnimann *et al.* 1992), eleven species belonging to the Trochamminina are here redescribed, and illustrated by scanning electron microscopy for the first time. The fauna has, for the most part, strong affinities with the foraminifera of brackish, mangrove sediments from other parts of the tropics, notably Brazil. Comparison is therefore made with material described by us (Brönnimann & Zaninetti, 1984a; b; Zaninetti *et al.*, 1977) from the mangroves of Guaratiba, Acupe and Baia de Sepetiba, Brazil.

For a recent review of mangrove foraminifera in general and their potential for palaeoenvironmental interpretation, the reader is referred to an important paper by Culver (1990).

LOCALITY INFORMATION

Of relevance to the present revision are the following stations from whence the specimens came; where the name of the station is not mentioned, the label has become illegible. The sample descriptions are in Durrand's own words.

Area 1 Station 2 [no locality]. Plastic mud, brownish tinted, rich in floatings.

† Deceased 6.1.1993.

Station 3 [no locality]. Brownish mud with lumps of blueish clay throughout, residue about one quarter-pound and floatings small.

Station 5 [no locality]. Blue ooze, residue and floatings small.

Station 9 [no locality]. Results poor.

Station 11 [no locality].

Station 12 [no locality].

Station 14. Similar to Station 13 [Segaar, New Guinea, coral sand and mud, residue about six ounces, floatings rich].

Station 15 [no locality].

Area 2 Station 17. Muntok Banka, blue mud, residue eight ounces, floatings rich.

Station 19 [no locality]. Earthy coloured, river-looking mud, few foraminifera.

Station 21. Paney, northeast coast of Sumatra.

Station 27 [no locality].

Station 28 [no locality].

Durrand (1898:257) adds a postscript, stating that . . . 'it is important to bear in mind all this series was obtained from shallow water close inshore . . .'. It is clear from the agglutinating foraminifera revised here, that most of the localities were in fact brackish, associated with mangroves.

SYSTEMATIC DESCRIPTIONS

Order **FORAMINIFERIDA** Eichwald, 1830

Suborder **TROCHAMMININA** Brönnimann & Whittaker, 1988

Apart from the hierarchy listed above, no further suprageneric taxa will be used. Until we can be certain that the families and superfamilies of agglutinating foraminifera used by Loeblich & Tappan (1987) represent homogeneous units with respect to the wall structure, then it is better, for the present, not to use them. Similarly, genera are used in 'inverted commas' when the wall structure of their type species has not yet been examined. The eleven species described here, at least, all have a Trochamminina-type wall, defined by Brönnimann & Whittaker (1988) as . . . 'consisting of organic and agglutinated phases. Agglutinant bound by organic cement and outer and inner organic sheets. Devoid of perforations or alveolar pseudopores'.

The synonymies are not meant to be comprehensive, they are selective, merely listing the original reference, junior synonyms, changes of generic combination and important citations from the study area.

Genus **ACUPEINA** Brönnimann & Zaninetti, 1984b

TYPE SPECIES. *Haplophragmium salsum* Cushman & Brönnimann, 1948a (= junior subjective synonym of *Haplophragmium agglutinans* d'Orbigny var. *triperforata* Millett, 1899).

***Acupeina triperforata* (Millett, 1899) Figs 1.2, 13–15**

1899 *Haplophragmium agglutinans* d'Orbigny var. *triperforata* Millett: 358(pars); pl. 5, figs 2a,b (lectotype) only; non figs 3a,b.

1948a *Haplophragmium salsum* Cushman & Brönnimann: 16,17; pl. 3, figs 10–13.

1965 *Lituola salsa* (Cushman & Brönnimann); Brönnimann & Zaninetti: 608–615; figs 1–3.

1984b *Acupeina salsa* (Cushman & Brönnimann); Brönnimann & Zaninetti: 219–222; figs A1–4, B1,2.

1984b *Acupeina triperforata* (Millett); Brönnimann & Zaninetti: 222 (addendum).

1988 *Acupeina triperforata* (Millett); Brönnimann & Whittaker: 112; pl. 4, figs 1–7.

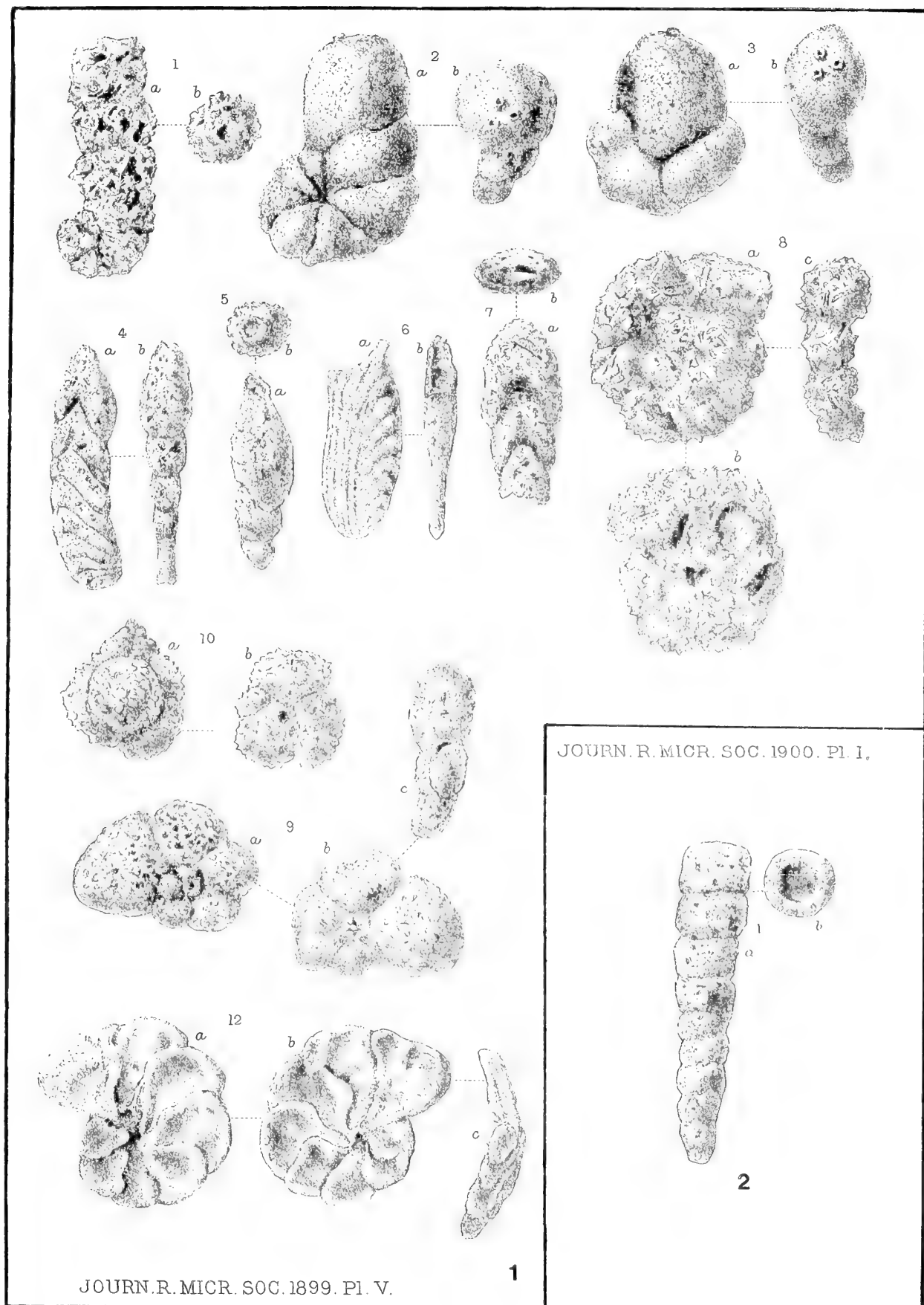
REMARKS. Millett (1899, pl. 5, figs 2,3; here reproduced as Figs 1.2, 3) illustrated four views of his new variety *triperforata*. Examination of the original material shows that two different brackish species are involved: *Acupeina triperforata* (Millett) and *Arenoparrella mexicana* (Kornfeld).

The individual drawn by Millett (1899, pl. 5, figs 2a,b; here reproduced in Fig. 1.2a,b) in side and apertural views, has been re-illustrated by SEM in Figs 13–15. The micrographs show side and edge views of a test, initially streptospiral then uniserial, and the detail of the multiple aperture which consists of three closely spaced, virtually equidistant pores (of around 25 µm diameter) with upturned rims. Millett apparently believed that the aperture of his new variety invariably consisted of the three rounded pores, hence the name. The individual in Figs 13–15 is undoubtedly Millett's figured specimen and is here formally designated lectotype.

The specimen drawn by Millett (1899, pl. 5, figs 3a,b; reproduced here in Fig. 1.3a,b) in side and apertural views, has been re-illustrated by SEM in Figs 9–12 not only to show both sides of the test but the details of the composite aperture. Its morphology is quite different from the lectotype of *H. agglutinans* var. *triperforata*. It represents, in fact, a typical specimen of *Arenoparrella mexicana* (Kornfeld, 1931)(see below). It is unfortunate that Loeblich & Tappan (1987: 21, pl. 71, figs 3,4) illustrated this very specimen, together with the lectotype, as *A. triperforata*. It is also worth noting that Millett's pl. 5, fig. 3b is the edge view of fig. 3a, but as can be seen from our SEM illustration, rather misleading. It purports to show only three large pores with everted borders. In reality, it has a single oblique-perpendicular slit and 12 small peripheral pores of 5–6 µm diameter, devoid of rims. Closer examination of Millett's apertural view (see Fig. 1.3b) may just show the termination of the slit (the specimen is tilted forward), but the determination of the pores is still seriously in error.

Fig. 1.1–1.10, 1.12 Reproduction of part of Plate 5 of Millett (1899). The original identifications were as follows: Fig. 1.1, *Haplophragmium agglutinans* (d'Orbigny), ×112; Fig. 1.2, 3, *H. agglutinans* var. *triperforata* var. nov., ×112; Fig. 1.4–6, *H. cassis* (Parker), ×112; Fig. 1.7, *H. cassis* (Parker) or ?*Reophax*, ×75; Fig. 1.8, *H. compressum* Goës, ×75; Fig. 1.9, *H. nanum* Brady, ×112; Fig. 1.10, *H. anceps* Brady, ×56; Fig. 1.12, *Trochammina ochracea* (Williamson), ×75. Reproduced by permission of the Royal Microscopical Society.

Fig. 2.1 Reproduction of part of Plate 1 of Millett (1900). It was originally identified as *Bigennerina digitata* d'Orbigny var., ×169. Reproduced by permission of the Royal Microscopical Society.



Brönnimann & Zaninetti (1984b: 222, Addendum) have shown that *Haplophragmium agglutinans* d'Orbigny var. *tripperforata* Millett (1899) is identical with *H. salsum* Cushman & Brönnimann (1948a), which is the type species of *Acupeina* Brönnimann & Zaninetti, 1984b.

LECTOTYPE. The individual illustrated by Millett (1899, pl. 5, figs 2a,b; Figs 1.2, 13–15 herein) is designated lectotype of *H. agglutinans* var. *tripperforata*, now *Acupeina tripperforata*. It is deposited in the collections of the BMNH, no. 1955.11.1.1076.

DIMENSIONS (LECTOTYPE). Height of test — 380 µm; diameter of coiled portion — 235 µm; maximum diameters of apertural pores — 25 µm, with everted rims 4 µm high.

ENVIRONMENT. This species . . . 'is not uncommon at Station 9, and occurs also, but very sparingly, at Station 5' of Area 1. At Station 9, Millett (1899: 359) also reported *Haplophragmium cassis* (Parker) (= *Ammoastuta salsa* Cushman & Brönnimann and *Ammotium* spp.), all brackish water species. Both *Acupeina tripperforata* and *Arenoparella mexicana* are also exclusively brackish forms, occurring commonly in tropical to subtropical mangrove swamp sediments.

Genus **AMMOSASTUTA** Loeblich & Tappan, 1984

TYPE SPECIES. *Ammoastuta salsa* Cushman & Brönnimann, 1948a.

***Ammoastuta salsa* Cushman & Brönnimann, 1948a**

Figs 1.6, 35

1899 *Haplophragmium cassis* (Parker); Millett (*pars*): 359; pl. 5, figs 6a,b only (*non* figs 4,5,7) (*non Lituola cassis* Parker, 1870).

1948a *Ammoastuta salsa* Cushman & Brönnimann: 17; pl. 3, figs 14–16.

1970 *Ammoastuta salsa* Cushman (*sic*); Hofker: 3.

1986 *Ammoastuta salsa* Cushman & Brönnimann; Brönnimann: 29–44; figs 1–7. (*q.v.* for synonymy).

REMARKS. Millett (1899: 359, pl. 5, figs 6a,b; here reproduced as Fig. 1.6a,b) figured side and edge views of a slightly damaged, but clearly recognizable specimen of *Ammoastuta salsa* under the name of *Haplophragmium cassis* (Parker). He also illustrated two different species of *Ammotium* (pl. 5, figs 4a,b, 5a,b; Figs 1.4, 5) and, used for all these different morphologies the same name, as he thought . . . 'the Malay specimens of this species [*H. cassis*] are very variable in form, some of them being extremely compressed, and composed of numerous chambers'.

The SEM photograph of the side view (Fig. 35), although now slightly more damaged, is demonstrably of the same specimen as in Millett's drawing. The tight initial coil cannot be seen, but on the other hand, the final two chambers of the

juvenile stage are clearly visible. The adult consists of at least 7 elongate uniserial chambers which make up the main portion of the compressed test.

Brönnimann's (1986) morphological revision of *A. salsa* has shown that the test starts with a tight early spiral consisting only of a proloculus and deuterolocus. On the basis of this arrangement, *Ammoastuta* is correctly placed in the Lituolidae. Loeblich & Tappan (1987: 79) accepted this interpretation, but stated that the second chamber is growing in the . . . 'opposite direction' (without saying in respect to what). This is simply not the case. The second chamber develops from a porus in the side of the proloculus. It is just the normal forward continuation, considering the flow of the protoplasm, which produces the elongate deuterolocus with a porus at its apex. Hence the embryonic chambers form a tight, reduced spiral (see Brönnimann, 1986: 32, fig. 3).

Ammoastuta salsa is occasionally placed in synonymy with *Ammobaculites* (= *Ammoastuta*) *ineptus* Cushman & McCulloch, 1939. Cushman & Brönnimann (1948a) regarded the two as distinct, as did Brönnimann (1986). An examination by Brönnimann of the two paratypes of *A. ineptus*, deposited in the collections of the U.S. National Museum of Natural History, Washington, confirms this separation. Of the paratypes, only one, registration no. 35826, is well preserved. It is definitely an *Ammoastuta*, but differs from the compressed *A. salsa* by having a strongly inflated test.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1121). Maximum height (damaged) — 280 µm.

ENVIRONMENT. Recorded from Station 9, Area 1. It occurs together with *Acupeina tripperforata*, *Ammotium* spp. and *Arenoparella mexicana*, all typical brackish water species.

Genus **AMMOBACULITES** Cushman, 1910

TYPE SPECIES. *Spirolina agglutinans* d'Orbigny, 1846. Lectotype designated by Loeblich & Tappan (1964: C241, figs 251.6a,b).

REMARKS. The genus *Ammobaculites* Cushman (1910) contains free agglutinated tests with a simple interior; the early portion is planispiral, the later part uncoiled and rectilinear. It is radially-symmetrical in transverse section. The single aperture is terminal, areal and radially symmetrical. The wall structure of the type species is unknown.

This definition is more restrictive than Loeblich & Tappan's (1987: 74) as it not only excludes streptospiral and trochospiral initial coils, but also laterally compressed tests. The transverse sections of the chambers of the uncoiled portion of the test and the outlines of the terminal apertures are radially symmetrical; these features are regarded as important generic criteria.

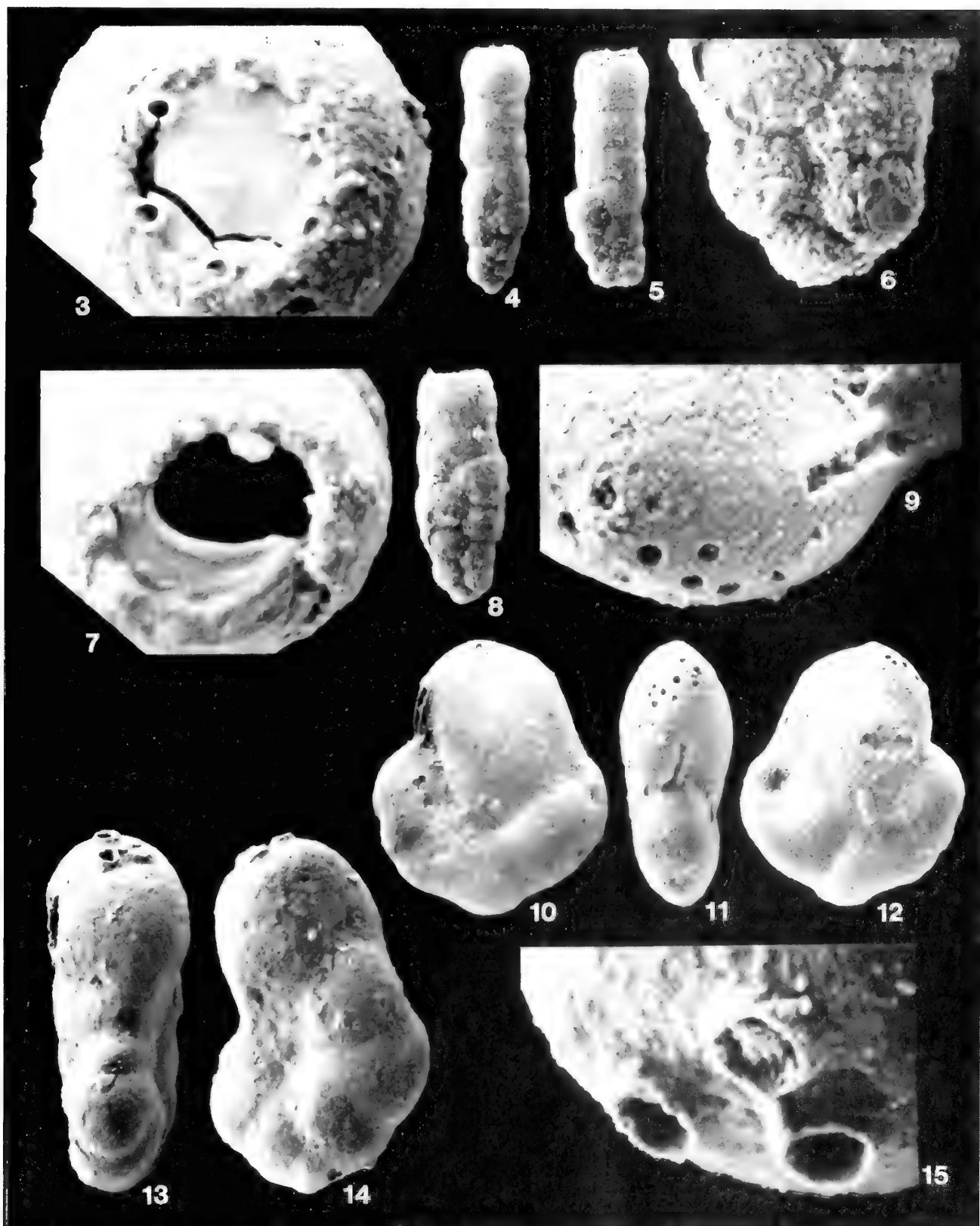
The wall structure of *Ammobaculites exiguus*, the species in the Millett Collection, is of the Trochammina type. If *A.*

Figs 3–8 *Trunculocavus durrandi* gen. et sp. nov. Figs 3.4, Detail of aperture (×900) and side view (×160), respectively. Holotype, BMNH no. 1955.11.1.187; Fig. 5, Side view (×175). Paratype, BMNH no. 1911.11.1.189; Figs 6–8, Detail of initial coil (×540), aperture (×730) and side view (×160), respectively. Paratype, BMNH no. 1955.11.1.188.

Figs 9–12 *Arenoparella mexicana* (Kornfeld). Detail of apertures (×480), side, edge and view of other side (×160), respectively. BMNH no. 1955.11.1.1075.

Figs 13–15 *Acupeina tripperforata* (Millett). Edge and side view (×160) and detail of aperture (×700), respectively. BMNH no. 1911.1.1.1076.

All from the Millett Collection, Malay Archipelago.



agglutinans, the type species, should have the same wall type, then *exiguus* would be correctly placed in *Ammobaculites*. If not, then it would have to be placed in a new genus. In view of these uncertainties, *Ammobaculites* is placed in inverted commas in our treatment of 'A'. *exiguus*.

'Ammobaculites' *exiguus* Cushman & Brönnimann, 1948b Figs 1.1, 42–44

- 1885 *Haplophragmium agglutinans* (d'Orbigny); Balkwill & Wright: 330; pl. 13, figs 18?, 19, 20 (*non* d'Orbigny, 1846).
 1899 *Haplophragmium agglutinans* (d'Orbigny); Millett: 357, pl. 5, figs 1a, b.
 1938 *Ammobaculites agglutinans* (d'Orbigny); Bartenstein: 391; fig. 14.
 1948b *Ammobaculites exiguus* Cushman & Brönnimann: 38; pl. 7, figs 7, 8.
 1952b *Ammobaculites* cf. *exiguus* Cushman & Brönnimann; Parker: 443; pl. 1, figs 16, 17.
 1952 *Ammobaculites agglutinans* (d'Orbigny); Rottgardt: 180; pl. 1, fig. 4. 1954 *Ammobaculites exiguus* Cushman & Brönnimann; Phleger: 633; pl. 1, fig. 5.
 1956 *Ammobaculites* sp. B, Warren: 139; pl. 1, figs 22–24.
 1957 *Ammobaculites exiguus* Cushman & Brönnimann; Todd & Brönnimann: 23; pl. 2, fig. 7.
 1962 *Ammobaculites exiguus* Cushman & Brönnimann; Benda & Puri: 335; pl. 1, fig. 15. 1973 *Ammobaculites balkwilli* Haynes: 25–27; pl. 2, figs 2, 3; pl. 29, figs 5, 6; text-fig. 4.1–5.
 1978 *Ammobaculites dilatatus* (*sic*) Cushman & Brönnimann; Schafer & Cole: pl. 3, fig. 9 (*non* Cushman & Brönnimann, 1948b).
 1980 *Ammobaculites dilatatus* Cushman & Brönnimann; Scott & Medioli: 35; pl. 1, figs 9, 10.
 ?1983 *Ammobaculites exiguus* Cushman & Brönnimann; Haman: 72; pl. 5, figs 1–4.
 1983 *Ammobaculites diversus* Cushman & Brönnimann; Haman: 72; pl. 4, figs 14, 15 (*non* Cushman & Brönnimann, 1948b).
 1986 *Ammobaculites exiguus* Cushman & Brönnimann; Brönnimann & Keij: pl. 3, fig. 7.

REMARKS. Millett (1899: pl. 5, figs 1a, b; here reproduced as Figs 1.1a, b) illustrated, without description, a typical specimen of *exiguus* under the name of *Haplophragmium agglutinans* (d'Orbigny). The same specimen (BMNH no. 1955.11.1.1057) is re-illustrated by SEM in our Figs 43, 44. The oblique view (Fig. 43) shows the radially-symmetrical areal and terminal aperture, which is larger than in Millett's drawing. It is not bordered by a rim as that shown by Haman's (1983, pl. 5, figs 1–4) 'A. *exiguus*', which may represent a different species. Millett's specimen has four uniserial chambers which follow from a planispiral, tightly enrolled early test. The agglutinant is coarse and the sutures in the initial portion are not well defined; on the uniserial portion, they are distinct, however, and run perpendicularly to the elongate axis of the test.

Illustrated in Fig. 42 (BMNH no. 1911.11.1.1058) is a smaller, albeit damaged specimen, which is more typical of the size of the Malay material. Four radial sutures can be recognized in the coiled portion and there are three chambers in the uniserial part; the final chamber is crushed.

One of us (P.B.) has re-examined the holotype of A.

exiguus (registration no. 56761) in the U.S. National Museum of Natural History. Its overall morphology corresponds well with Millett's illustrated specimen of *H. agglutinans*. However, in its uniserial portion there are five chambers and the agglutinant is finer than in the Malay specimen. Nevertheless, the two both have a circular transverse section and a large radially-symmetrical, terminal aperture without a rim; the intercameral sutures run perpendicular to the elongate axis of the test, there being no suggestion of *Ammotium*-type sutures. In addition to the holotype of *exiguus*, there are two slides with paratypes: in slide no. 56762 there is a single paratype; under no. 56763 there are, amongst typical specimens, some very small individuals which differ from the type by their thin, elongate tests. These latter have also been encountered by us in the mangrove sediments of Açupe, Brazil. They represent a new species of brackish 'Ammobaculites' which will be published elsewhere. It should be noted that 'A'. *exiguus* and this new, minute species, are the only true representatives of 'Ammobaculites' occurring in brackish waters.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1911.11.1.1057). Height of test — 385 µm; diameter of initial planispiral portion — 135 µm; diameter of final chamber — 125 µm; diameter of aperture — 50 µm.

ENVIRONMENT. In the Millett Collection, specimens are labelled '*Haplophragmium agglutinans*' from stations 2, 9, 12, 14, 15, 19, 21 and 27; Millett notes (p. 358) that . . . 'the specimens are all minute, and although they occur at most of the Stations, are not very numerous'. According to Parker *et al.* (1953), 'A'. *exiguus* is a species which lives in brackish as well as in marine waters.

Genus *AMMOTIUM* Loeblich & Tappan, 1953

TYPE SPECIES. *Lituola cassis* Parker (*in* Dawson), 1870.

REMARKS. *Ammomarginulina* Wiesner, 1931 (type species: *A. ensis* Wiesner, 1931) is a deep-water genus, with a morphology close to that of the supposedly exclusively brackish-water genus, *Ammotium*. After having compared the definitions of *Ammomarginulina* and of *Ammotium* in Loeblich & Tappan (1987), the question arises as to whether the two are really synonymous. The sutures of the former are, however, less slanting than those of *Ammotium*, and the test is strongly compressed. Of the shape of the aperture of *Ammomarginulina ensis* nothing is known except for the fact that it is rounded. Small morphological differences such as these may not be considered sufficient to retain the two genera. However, they seem to represent two disparate homogeneous environmental groups which, should this be sustained, must be separated taxonomically, even if the morphological differences were even less pronounced (see also Resig's (1982: 977–978, pl. 1, figs 3–5, 9) description of *Ammomarginulina hadalensis* Resig from the Peru-Chile Trench, depth 5846 m). Clearly, the wall structure of *Ammomarginulina* must also be investigated.

***Ammotium morenoi* (Acosta, 1940) Figs 32–34, 54**

- 1899 *Haplophragmium cassis* (Parker): 359 (*pars*) (*non* *Lituola cassis* Parker, 1870).
 1940 *Ammobaculites morenoi* Acosta: 272; pl. 49, figs 3, 8 (holotype) only (*non* Fig. 1).

- 1948a *Ammobaculites salsus* Cushman & Brönnimann: 16; pl. 3, figs 7a,b,8,9 (holotype figs 7a,b).
- 1952b *Ammoscalaria fluvialis* Parker: 444; pl. 1, fig. 24 (holotype) only (*non* fig. 25).
- 1953 *Ammobaculites salsus* (*et vars.*) Parker *et al.*: 5; pl. 1, figs 18–25 only (*non* fig. 17).
- 1954 *Ammobaculites exilis* Cushman & Brönnimann; Phleger: pl. 1, fig. 6 (*non* Cushman & Brönnimann, 1948b).
- 1954 *Ammobaculites salsus* Cushman & Brönnimann; Phleger: pl. 1, fig. 7 only (*non* fig. 8).
- 1954 *Ammoscalaria fluvialis* Parker; Phleger: pl. 1, fig. 11.
- 1957 *Ammobaculites salsus* Cushman & Brönnimann; Todd & Brönnimann: 24, pl. 3, fig. 8.
- 1958 *Ammobaculites salsus* Cushman & Brönnimann; Arnal: 37; pl. 98, figs 4–7.
- 1968 *Ammotium salsum* (Cushman & Brönnimann); Lutze: 25; pl. 1, figs 5,6.
- 1978 *Ammotium salsum* (Cushman & Brönnimann); Poag: 405; pl. 5, figs 1–39.
- 1980 *Ammotium salsum* (Cushman & Brönnimann); Scott & Medioli: pl. 1, figs 11–13.
- 1983 *Ammotium morenoi* (Acosta); Haman: 72; pl. 5, figs 6–9.

REMARKS. The specimen illustrated by us in Figs 32–34 was not figured or described by Millett but comes from a slide in the Millett Collection labelled *Haplophragmium cassis* Parker (BMNH no. 1955.11.1.1118–1133) and was undoubtedly part of his concept of that species. It is a typical representative of *Ammotium morenoi*. The small test is axially compressed and consists of a short, completely coiled planispiral initial stage, followed by an uncoiled portion of about 5 low, elongate, laterally compressed chambers which on the interior side reach back toward the initial planispire. The single aperture is a narrow elongate slit with rounded extremities, situated at the apex of the final chamber, in a marginal or outer position.

Under the name of *H. cassis*, Millett (1899, pl. 5, figs 4a,b, 5a,b) did illustrate two specimens, which belong to different species of *Ammotium*. The latter (reproduced here as Fig. 1.5a,b) is the upper part of an *Ammotium pseudocassis* (Cushman & Brönnimann, 1948b) (see p. , below) but was not found in the Millett Collection. The former (Fig. 1.4a,b) is a complete specimen of *A. directum* (Cushman & Brönnimann, 1948b) and is refigured in Fig. 31.

In addition to this specimen, we have also illustrated in Fig. 54, for the purpose of comparison, the lateral view of a typical specimen of *A. morenoi* from the mangrove sediments of Guaratiba, Brazil (see Zaninetti *et al.*, 1977). It consists of an initial, almost involute planispire, followed by two uniserial, laterally flattened, low and elongate chambers, which on the inner side extend backwards toward the early spire.

In common with other brackish foraminifera, *A. morenoi* is highly variable in its overall morphology, in particular in size and in outline of the test in lateral view. From small, almost triangular forms, as represented by the holotype of *morenoi* or the holotype of *Ammoscalaria fluvialis* Parker (1952b), we find all possible transitions to the elongate slender specimens of *Ammobaculites salsus* described by Cushman & Brönnimann (1948a) from Trinidad, or to the large and elongate individuals recorded by Poag (1978) from Gulf Coast estuaries. Brodniewicz (1965: 187–194, text-figs 21–25) has shown that a similar form, identified by her as *Ammotium cassis* (Parker), from the Baltic, is also characterized by a great

morphological variability. She tried to distinguish six different morphological types on the basis of outline, chamber form, and dimensions of the test and chambers. A study of Brodniewicz's paper, however, suggests to us that it is virtually impossible to separate her different morphotypes.

DIMENSIONS OF FIGURED SPECIMENS (MALAY SPECIMEN, BMNH no. 1991.11.1.1122). Height of test — 170 µm; width (length) — 105 µm; thickness — 35 µm.

(BRAZILIAN SPECIMEN). Height of test — 370 µm; maximum width — 190 µm; final chamber — 225 µm high; maximum diameter of oblong aperture — 50 µm.

ENVIRONMENT. Found only in Station 9 (Area 1) in association with *Ammotium pseudocassis*, *A. directum*, *Acupeina triperforata*, *Ammoastuta salsa* and *Arenoparella mexicana*, all typical brackish water species. *A. morenoi* is normally abundant in tropical and subtropical mangrove sediments but has also been recorded, albeit rarely, in brackish sediments of temperate climes (Parker, 1952b; Lutze, 1968). We have never encountered this species in the British Isles or in the Mediterranean.

OBSERVATIONS ON CERTAIN SYNONYMS AND NON-SYNONYMS (NEAR ISOMORPHS) OF *AMMOTIUM MORENOI* ACOSTA.

1. *Ammobaculites salsus* Cushman & Brönnimann, 1948a and *A. distinctus* Cushman & Brönnimann, 1948b.

Haman (1983) was the first author to place *Ammobaculites* (= *Ammotium*) *salsus* into synonymy with Acosta's species. In the introduction to his paper, Acosta (1940: 269) wrote that the agglutinating species were rare in the shallow water assemblages from the Gulf of Santa Maria, Camaguey Province, Cuba, which were dominated by miliolids and nonionids. The Gulf of Santa Maria is bordered by extensive mangrove swamps. It is therefore assumed that the tests of the brackish agglutinated species, such as *A. morenoi*, had been transported by wave action into the marine environment of the open Gulf and were not *in situ* at the locality where Acosta collected them. Acosta (1940: 275) claimed to have deposited the types of his species in the Cushman Collection, which were later transferred from Sharon, Massachusetts to the U.S. National Museum of Natural History, Washington, D.C. A search by P.B. for the type specimen of *A. morenoi* proved unsuccessful and it seems that Acosta never did deposit his types in the Cushman Collection. Acosta's drawings (*op.cit.* pl. 49, figs 3,8, *non* fig. 1) leave no doubt, however, that *Ammotium morenoi* and *A. salsum*, originally described from Trinidad mangrove swamps, are one and the same.

When comparing the two 'species', the apertural view of the holotype of *Ammotium morenoi* (Acosta, 1940: pl. 49, fig. 8) is of interest. It shows a slit-like opening at the apex of the final chamber, in a marginal or outer position; the same type of aperture occurs in *A. salsum*. In both holotypes the peripheral outline of the initial planispire, as seen laterally, is perfectly rounded and not angular as in *Ammotium distinctum* (Cushman & Brönnimann (1948b: 40, pl. 7, fig. 14), which has also been described from the brackish mangrove sediments of Trinidad. This latter form was originally introduced as a variety of *Ammobaculites salsus*. As there are no intermediates between *distinctum* and *salsum*, the former is here elevated to specific rank. Authors, however, normally

make no distinction between the two (see Phleger, 1954: pl. 1, fig. 8).

We have illustrated in Fig. 55 a lateral view in oil of *Ammotium distinctum*, from the mangrove sediments of Acupe, Brazil. The angular outline of the early planispire is clearly shown. The test begins with a relatively large proloculus of 65 µm diameter, followed by a larger deuterochamber of 75 µm diameter. The total number of chambers in this specimen is eight, including the embryonic chambers. The height of the test is 220 µm, width (length) 125 µm, and length of aperture 45 µm. Apart from the distinct angular periphery, there are no other important differences between *Ammotium morenoi* and *A. distinctum*.

2. *Ammoscalaria fluvialis* Parker, 1952b.

Parker (1952b: 444, pl. 1, fig. 24) first described this species from the Housatonic River, Long Island Sound, depth 3 m. From its association with other brackish species in her Facies 1, such as *Trochammina inflata*, *Jadammina macrescens* and *Miliammina fusca*, it can be inferred that *A. fluvialis* is also a brackish-water form. The morphology of the holotype is virtually identical with the holotype of *A. morenoi*, and for this reason we regard it as a junior synonym of the latter.

3. *Lituola cassis* Parker, in Dawson, 1870.

We have compared *Ammotium morenoi* with *Lituola cassis* Parker, the type species of *Ammotium* Loeblich & Tappan (1953). The lectotype of *Ammotium cassis* (BMNH no. ZF 4637), designated by Hodgkinson (1992), on our advice, is re-illustrated in Figs 38–41. It is from Gaspé Bay, Gulf of St. Lawrence, Canada, and came from the W.K. Parker Collection; it was collected in 16 fathoms (30 m), which suggests a marine environment, but the specimens could have been washed in from a brackish locality. Loeblich & Tappan (1987, pl. 60, figs 1,2) illustrate a 'Holocene' specimen from off Alaska in 223 m of water; should this specimen have been *in situ* it would further undermine the supposedly exclusively brackish nature of the genus, a factor that needs further investigation.

The lectotype clearly shows the initial planispire, then the uniserial inward slanting narrow and low chambers; the oblong aperture is at the apex of the final chamber, in a marginal or outer position (see also Goës, 1894, pl. 5, figs 152–157). The lectotype and paralectotypes are five times larger and much more massive than *A. morenoi*, though the two in several other respects are quite similar. It is our opinion that *A. cassis* should only be used for large and massive individuals, but at the same time we have our reservations that ecological factors (?marine salinities) may be responsible for the massive development of the *cassis* test (see also remarks above, on *A. cassis sensu* Brodniewicz (1965) from the Baltic). It is even three times the size of Poag's (1978) material from the Gulf Coast estuaries, the largest known specimens of *A. morenoi* from the tropics,

moreover Poag's specimens are very elongate and compressed with the uniserial portion quite unlike that of the true *cassis*.

The dimensions of the lectotype are: maximum height — 1600 µm; maximum width — 785 µm; maximum thickness — 360 µm; thickness of planispiral portion — 125 µm.

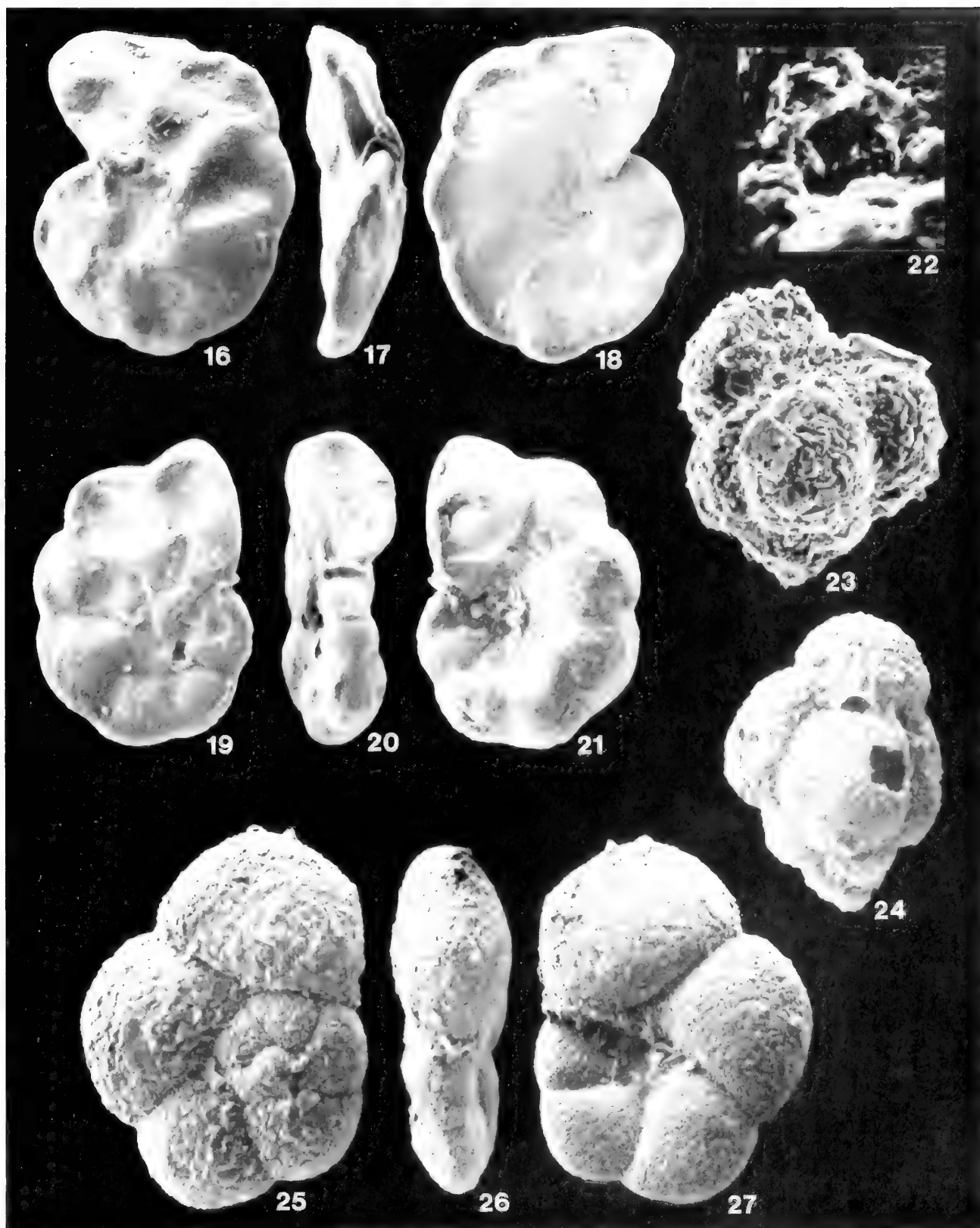
4. *Ammobaculites prostomum* Hofker, 1932.

This species was described by Hofker (1932: 87–91, text-figs 14a–f, 15a–d) from the Ammontatura, a part of the Gulf of Naples, with a depth of 150–200 m. The shapes of the illustrated specimens, seen laterally, particularly the short individuals (text-figs 14a and f), much resemble the small specimens of *Ammotium morenoi* such as our Fig. 54. On Hofker's short specimens the sutures are not shown fully, but on the larger specimens (text-fig. 15e) they are, toward the outer margin, at first outward slanting (not inward), then parallel up to the end of the uniserial portion. In lateral outline, these short specimens are near isomorphs of *A. morenoi*. However, the aperture is not placed asymmetrically, at the outer margin of the test as in *Ammotium*, but symmetrically in respect to the shape of the final chamber. For these reasons, Hofker's species does not belong to *Ammotium*. It is also a marine species and much resembles the group pf forms described and illustrated by Höglund (1947, pl. 31, figs 1a–g) from Björkholmen, Gullmar Fjord, from a depth of 30 m, under the name of *Ammoscalaria pseudospiralis* (Williamson).

5. *Ammoscalaria pseudospiralis sensu* Höglund, 1947.

The genus *Ammoscalaria* was erected by Höglund (1947: 151–153) with *Haplophragmium tenuimargo* Brady (1884) as type species. Into his new genus he also placed *Proteonina pseudospiralis* Williamson, 1858. However, *Ammoscalaria pseudospiralis* was described by Höglund (1947: 159–162, pl. 31, figs 1a–p) exclusively from material obtained in the Gullmar Fjord, where it occurs commonly, and from the Skagerak, not on the basis of Williamson's material which was not available to him. The chambers of the rectilinear portion of this marine species are 'irregularly rectangular in lateral view' and there are 'no external sutures'. The oblong aperture is in a symmetrical position in respect to the final chamber and not asymmetric, as in *Ammotium*. We therefore do not regard Höglund's species as a synonym of *pseudospiralis*, although certain smaller specimens could be regarded as isomorphs of Williamson's taxon, particularly when seen in lateral view (e.g. pl. 31, figs 1m,n). Rather, Höglund's form is most probably a junior synonym of *Ammobaculites* (= *Ammoscalaria*) *prostomum* Hofker, 1932.

- Figs 16–21 'Haplophragmoides' wilberti Anderson. Figs 16–18, Side, edge and view of other side (×115). BMNH no. 1911.11.1.5003; Figs 19–21, Side, edge and view of other side (×160), respectively. BMNH no. ZF 5002. Specimen from Brönnimann sample BR146, Acupe, Brazil, for comparison.
- Figs 22–24 *Trochammina? milleti* sp. nov. Figs 22,23, Detail of aperture (×1,700) and side view (×320), respectively. Holotype, BMNH no. 1911.11.1.1088; Fig. 24, Side view (×260). Paratype, BMNH no. 1955.11.1.1089.
- Figs 25–27 *Paratrochammina simplissima* (Cushman & McCulloch). Spiral, edge and umbilical views (×170). BMNH no. 1955.11.1.1141. All from the Millett Collection, Malay Archipelago, except where stated.



Ammotium pseudocassis (Cushman & Brönnimann, 1948) Figs 1.5, 50, 53

- 1899 *Haplophragmium cassis* (Parker); Millett: 359 (*pars*); pl. 5, figs 5a,b only (*non Lituola cassis* Parker, 1870).
 1948b *Ammobaculites pseudocassis* Cushman & Brönnimann: 39, 40; pl. 7, figs 12a,b.
 1983 *Ammoscalaria pseudospiralis* (Williamson); Haman: 72; pl. 5, fig. 5 (*non Proteonina pseudospiralis* Williamson, 1858).

REMARKS. This species was illustrated by Millett (1899, pl. 5, figs 5a,b; here reproduced as Fig. 1.5a,b) under the name of *Haplophragmium cassis* (Parker). It is an upper fragment of an elongate test consisting of three rounded (in transverse section), hardly compressed chambers. Millett's drawing shows the inward and backward trending sutures and the rounded aperture in marginal position. Within the concept of this species, Millett also included specimens of *Ammotium directum* (Cushman & Brönnimann) (Figs 1.4a,b, 31, ?36) and *Ammoastuta salsa* Cushman & Brönnimann (Figs 1.6a,b, 35). As already mentioned, the fragment of *A. pseudocassis* illustrated by Millett in his pl. 5, figs 5a,b (see our Figs 1.5a,b) could not be found in his Malay collection.

For comparison, we have illustrated typical specimens in lateral view of *A. pseudocassis* from the mangrove sediments of Guaratiba, Brazil (see Zaninetti *et al.*, 1977), one by SEM (Fig. 50), the other by optical photography in immersion (Fig. 53). In the latter specimen the early spiral is reduced to two chambers, a relatively large proloculus of 50 µm diameter, and a larger deuteroecolus of about 75 µm diameter. The embryonic chambers are not enclosed by other spiral chambers, as in *A. pseudospirale* (Williamson, 1858). The total number of chambers, including embryonics, is eight.

Ammotium pseudocassis differs from *A. pseudospirale* by the elongate, somewhat incurved test, the less compressed and elongate chambers and the reduced initial spire. The final chamber is usually the dominant one, making up about one-third of the test. It narrows toward the oblong aperture and extends on the inner side of the test toward the initial spiral. The early coil, represented by a reduced spire, consists of very few chambers only. A typical embryo consists of two very thin-walled chambers, a large proloculus, about 40–60 µm in diameter, and an equally large deuteroecolus. The embryo may form all the initial portion of the test. We have never found a microspheric specimen of *A. pseudocassis* and where the taxon is frequent, *A. pseudospirale* is usually absent. The aperture of the holotype of *A. pseudocassis*, deposited in the U.S. National Museum of Natural History (registration no. 56764), is not as circular as that shown in Millett's drawing, but distinctly oblong. As in *Ammotium cassis* and *A. morenoi*, the aperture is situated at the apex of the last chamber in a marginal position (see Cushman &

Brönnimann, 1948b, pl. 7, fig. 12b). However, it seems that, when the final chamber is hardly compressed, the aperture may become rather centred and more rounded than slit-like, but never completely circular.

DIMENSIONS. Fig. 50: Height of test — 480 µm; maximum width — 150 µm; height of final chamber — 290 µm; maximum diameter of aperture — 50 µm.

Fig. 52: Height of test — 575 µm; maximum width — 170 µm; height of final chamber — 375 µm; maximum diameter of aperture — 75 µm; thickness of wall (final chamber) 10 µm.

ENVIRONMENT. The group of forms referred by Millett to *H. cassis* (Parker) occur only at Station 9, Area 1, . . . 'where they are not uncommon'. They are all exclusively brackish water species.

Ammotium directum (Cushman & Brönnimann, 1948b) Figs 1.4, (?1.7), 31, 36, 37, 45–47

- 1899 *Haplophragmium cassis* (Parker): 359 (*pars*); pl. 5, figs 4, ?7 only (*non Lituola cassis* Parker, 1870).
 1948b *Ammobaculites directus* Cushman & Brönnimann: 38; pl. 7, figs 3, 4.
 1956 *Ammotium* sp. D. Warren: 139; pl. 1, figs 19–21.
 1957 *Ammobaculites directus* Cushman & Brönnimann; Todd & Brönnimann: 23; pl. 2, fig. 6 only (*non* Fig. 7).
 1988 *Ammotium casamancensis* (*sic*) Debenay: 46, 47; pl. 1, figs 1–3.

REMARKS. Under the name of *H. cassis* (Parker), Millett (1899, pl. 5, figs 4a,b; here reproduced as Figs 1.4a,b) illustrated a specimen of *Ammotium directum* (Cushman & Brönnimann). Our identification is based on the overall outline, the shape of the sutures, and the strong lateral compression of the test. The specimen illustrated by SEM in Fig. 31 is that very same specimen, viewed from the other side.

The fragment shown in Millett's fig. 7, which he compared to . . . 'a species of *Reophax*, with the plan of growth and chevron-shaped chambers of *Fronicularia*' may be that illustrated by SEM in Figs 36, 45, 46, although the chevron-shaped chambers are exaggerated, as they are in the drawing of fig. 4a (compare with our Fig. 31). The aperture in both specimens is slit-like, without an everted border, and is situated at the apex of the final chamber. For comparative purposes, a lateral view of a specimen of *A. directum*, from the mangrove sediments of Acupe, Brazil (BMNH no. ZF 4999) is illustrated in Fig. 47; the asymmetrical sutures are well exhibited.

The tests of *Ammotium directum* in the Millett Collection are extremely fragile, in contrast to those found in Trinidad

Figs 28–30 *Trematophragmoides bruneiensis* Brönnimann & Keij. Side, edge and view of other side (×115). BMNH no. 1955.11.1.1136.

Figs 31, 36, 37 *Ammotium directum* (Cushman & Brönnimann). Side views of three separate specimens (×185, 205 and 185, respectively). BMNH nos. 1955.11.1.1118–1120.

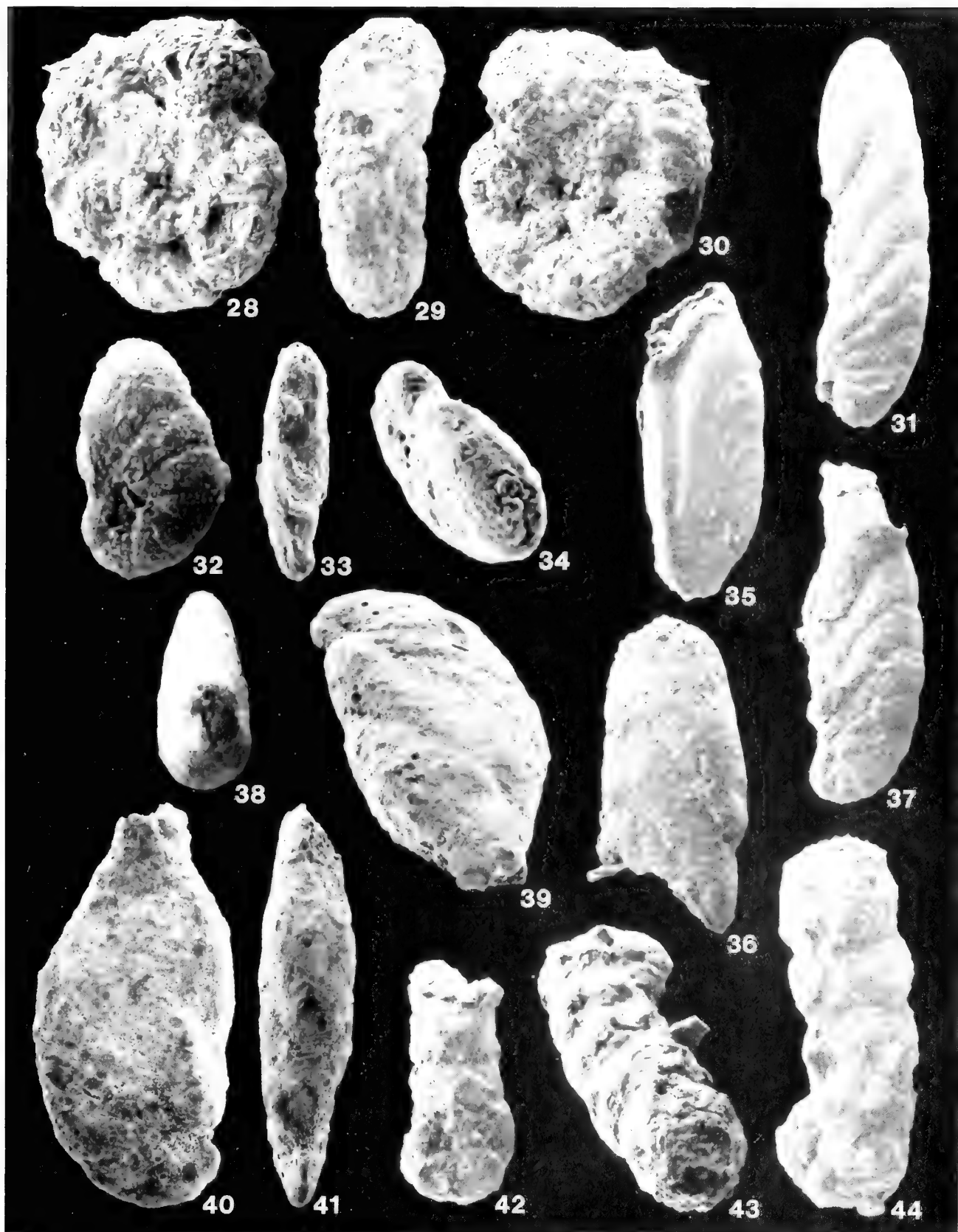
Figs 32–34 *Ammotium morenoi* (Acosta). Side, edge and oblique apertural views (×250). BMNH no. 1955.11.1.1122.

Fig. 35 *Ammoastuta salsa* Cushman & Brönnimann. Side view (×200). BMNH no. 1955.11.1.1121.

Figs 38–41 *Ammotium cassis* (Parker). Apertural, oblique apertural, side and edge views (×45). Lectotype, BMNH no. ZF 4637, Gaspé Bay, Gulf of St. Lawrence, Canada.

Figs 42–44 '*Ammobaculites*' *exiguus* Cushman & Brönnimann. Fig. 42, Side view (×185). BMNH no. 1955.11.1.1058; Figs 43, 44, Oblique-apertural and edge views (×175). BMNH no. 1955.11.1.1057.

All from Millett Collection, Malay Archipelago, except where stated.



or Brazil. Cushman & Brönnimann (1948b) distinguished two species of *Ammotium* with strong lateral compression, namely *A. directum* and *A. diversum*. To these has to be added a third, *A. subdirectum* Warren, 1956.

Ammotium directum, the more common species, as described above, has strongly incurved sutures of an asymmetrical type with a shorter outer or marginal branch and a longer, inner branch, which slants toward the initial spire (see Fig. 47). Occasionally, some sort of chevron pattern is formed but rarely to the extremes indicated by Millett's drawing (pl. 5, fig. 4a; our Fig. 1.4a). *A. directum* is always characterized by this asymmetrical type of suture. The test, moreover, is strongly compressed laterally and the width of the flattened chambers does not increase much in the course of growth. The aperture is slit-like and situated at the apex of the final chamber, more or less in a marginal position. The initial spiral consists of several chambers.

A. diversum is less common than *A. directum*. The only significant difference lies in the sutural shape, which in the former in the final ontogenetic stage, is always more or less horizontal, slightly incurved and in extremes, no longer asymmetrical (see Cushman & Brönnimann, 1948b, pl. 7, figs 5,6). Furthermore, in this species, the sutures of the early uniserial portion are slanting inward toward the initial coil. Occasionally, there is a suggestion that the two are linked by transitional forms. Should the two be ultimately considered synonymous then we would prefer to retain *A. directum*, as this, although printed on the same page, was described first. For the time being, however, both are retained.

A. subdirectum was described by Warren (1957, pl. 4, figs 6-8) from the marshes of the Buras-Scofield bayou region of southeastern Louisiana. We have encountered it but rarely in the mangrove sediments of Acupe, Brazil and Warren himself (1957: 33) mentioned that . . . 'specimens were rare wherever found except in one of the polyhaline marsh samples'. Two specimens from Acupe (BMNH nos ZF 5000 and 5001) are illustrated in Figs 48,49,51,52 for comparison with the Malay species of *Ammotium*. *A. subdirectum* is a many-chambered species characterized by the same asymmetrical type of sutures as found in *A. directum*. In the final growth stages the sutures may become more or less symmetrical and arranged in a chevron-like pattern, as shown in Millett's drawing of the fragment illustrated in pl. 5, figs 7a,b; Fig. 1.7a,b. Figs 36,45,46 could represent this specimen which is part of either an *A. subdirectum*, or an *A. directum* as discussed above. Normally, *A. subdirectum* is about twice as long as *A. directum* and composed of more chambers. The test is slightly incurved and the width of the chambers, seen laterally, increases quite strongly towards the final chamber. The aperture is a narrow oblong slit, as in *A. directum* and *A. diversum*, and situated at the apex of the final chamber, more or less in a marginal position (see Figs 48,49,51,52). In all three species, the agglutinant is fine-grained and the surface of the test usually appears smooth, occasionally even somewhat glossy.

DIMENSIONS OF FIGURED SPECIMENS (BMNH no. 1955.11.1.1118). Height of test — 290 µm; maximum width of final chamber — 73 µm.

(BMNH no. 1955.11.1.1119). Height of fragment — 270 µm; length of apertural slit — 45 µm.

(BMNH no. 1955.11.1.1120). Height of test — 330 µm.

ENVIRONMENT. This species was found only at Station 9

(Area 1). It is a typical brackish-water species.

Genus *ARENOPARRELLA* Andersen, 1951a

TYPE SPECIES. *Trochammina inflata* (Montagu) var. *mexicana* Kornfeld, 1931.

Arenoparrella mexicana (Kornfeld, 1931)

Figs 1.3, 9-12

1899 *Haplophragmium agglutinans* d'Orbigny var. *tripерforata* Millett: 358 (*pars*); pl. 5, figs 3a,b only; non figs 2a,b.

1931 *Trochammina inflata* (Montagu) var. *mexicana* Kornfeld: 86; pl. 13, figs 5a-c.

1951a *Arenoparrella mexicana* (Kornfeld); Andersen: 31; fig. 1a-c.

1951b *Arenoparrella mexicana* (Kornfeld); Andersen: 96; pl. 11, figs 4a-c.

1977 *Arenoparrella mexicana* (Kornfeld); Zaninetti *et al.*; pl. 2, figs 3,7.

REMARKS. One of Millett's illustrated specimens (1899, pl. 5, figs 3a,b; reproduced here as Figs 1.3a,b) of *H. agglutinans* var. *tripерforata* is, in fact, a typical specimen of *Arenoparrella mexicana* (Kornfeld). It is refigured here by SEM (Figs 9-12) and shows that the original drawing of the edge view in particular, is very misleading. As discussed above under the description of the lectotype of *Acupeina triperforata* (Millett), the edge view of fig. 3b also suggests that there are only three large everted apertures. The reality is an aperture consisting of a vertical slit lined by slightly uplifted borders, in an interior marginal position, of about 50 µm length and 8 µm width, and 12 small, irregularly arranged, rounded pores above this primary aperture, of between 5 and 10 µm diameter, devoid of everted rims. Millett's specimen (BMNH no. 1955.11.1.1075) is tilted so far forward in apertural view that the primary vertical slit, so clearly visible in fig. 3a, might not have been seen, but it is puzzling to understand why he illustrated the apertural pores as he did. Millett's material from stations 5 and 9 quite clearly represents both *Acupeina triperforata* and *Arenoparrella mexicana*, which is not surprising as they commonly occur together. The illustrated specimen of the latter is completely involute (hence the small axial depression is closed). The final whorl consists of 4, axially compressed chambers which gradually increase in size with growth. In edge view the periphery is rounded. Umbilical and spiral sutures are poorly defined and the agglutination is rather fine-grained and produces a smooth surface.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1075). Maximum diameter — 290 µm; minimum diameter — 240 µm; axial height (thickness) — 120 µm.

ENVIRONMENT. See under *Acupeina triperforata* (p.). *Arenoparrella mexicana* is a typical tropical and subtropical mangrove swamp species.

Genus *HAPLOPHRAGMOIDES* Cushman, 1910

TYPE SPECIES. *Nonionina canariensis* d'Orbigny, 1839.

REMARKS. The wall structure of the type species is unknown; we are not even sure of the apertural position, for that matter. Although the wall of *H. wilberti*, the species in the

Millett Collection, is of the *Trochammina*-type (see below), we prefer, in our treatment of this species, to use *Haplophragmoides* in inverted commas, until more is known about *canariensis*.

'Haplophragmoides' wilberti Andersen, 1953

Figs 1.12, 16–21

- 1899 *Trochammina ochracea* Williamson; Millett: 363, pl. 5, figs 12a–c (*non* Williamson, 1858).
 1953 *Haplophragmoides wilberti* Andersen: 21, pl. 4, figs 7a,b.
 1961 *Haplophragmoides wilberti* Andersen; Todd & Low: 133; pl. 1, fig. 5.
 1973 *Haplophragmoides wilberti* Andersen; Haynes: 27–30, pl. 2, fig. 1; pl. 29, fig. ??; text-figs 5.3–7.
 1977 *Haplophragmoides wilberti* Andersen; Zaninetti *et al.*: pl. 1, figs 12,13.
 1981 *Trochammina* sp., Cann & de Deckker: 668, pl. 2, figs 1–19.
 1983 *Haplophragmoides wilberti* Andersen; Haman: 71; pl. 3, figs 14,15.

REMARKS. On re-examination, Millett's (1899, pl. 5, figs 12a–c; reproduced here as Figs 1.12a–c) so-called *Trochammina ochracea* proved to be a planispiral '*Haplophragmoides*'. It is re-illustrated by SEM in Figs 16–18 and it (BMNH no 1955.11.1.5003) clearly shows the same collapse features as the original drawings. In addition to this specimen, we have illustrated for comparative purposes (Figs 19–21), another, somewhat less deformed specimen, from Acupe, Brazil (BMNH no. ZF 5002).

The coiling of Millett's species is planispiral, virtually involute, with 7 or 8 chambers in the final whorl. The aperture is a single interiomarginal equatorial slit with a broad everted border. The intercameral sutures are incurved, occasionally sinuous. We are placing it into the widespread brackish form, '*H.* *wilberti* Andersen. Millett must have regarded it as a *Trochammina* because of the incurved test seen in edge view.

Cann & de Deckker (1981, pl. 2, figs 1–19) illustrated from ephemeral lakes adjacent to the Coorong Lagoon, South Australia, a series of haplophragmoid forms, in part deformed, which they called *Trochammina* sp. They are very similar to *T. ochracea sensu* Millett and we have also placed them in '*H.* *wilberti*.

Collapse features occur often in brackish foraminifera. The overall consistency of the agglutinated phase, in particular its thickness and cementation, seems to play a role. In the deformed Millett material it appears that the agglutinated phase is rather weakly developed. In non-deformed specimens of '*H.* *wilberti*', at our disposal, from brackish localities in Nigeria and New Guinea, the wall structure was analysed using high-resolution scanning electron microscopy of fractured tests. It was found that the wall of these specimens is made up of the organic phase (represented by thin inner and outer sheets and material ('glue') between agglutinated elements), and the agglutinated phase. There were no perforations nor alveolar pseudopores present. This is the characteristic *Trochammina*-type wall. In these latter, non-deformed specimens, the agglutinated phase appears to be stronger, perhaps better cemented, than the Millett material from the Malay Archipelago.

DIMENSIONS OF FIGURED SPECIMENS (MALAY SPECIMEN,

BMNH no. 1955.11.1.5003). Maximum diameter — 490 µm; axial height (thickness) — 125 µm.

(BRAZILIAN SPECIMEN, BMNH no. ZF 5002). Maximum diameter — 340 µm.

ENVIRONMENT. According to Millett (1899; 363) this species . . . 'has been observed only at Station 3'. It is a good brackish water indicator and occurs in association with *Trematophragmoides bruneiensis* at this locality.

Genus **PARATROCHAMMINA** Brönnimann, 1979

TYPE SPECIES. *Paratrochammina madeirae* Brönnimann, 1979

Paratrochammina simplissima (Cushman & McCulloch, 1948) Figs 1.9, 25–27

- 1899 *Haplophragmium nanum* Brady; Millett: 360; pl. 5, figs 9a–c (*non* Brady, 1881).
 1939 *Trochammina pacifica* Cushman var. *simplex* Cushman & McCulloch: 104; pl. 11, fig. 4 (*non* Friedburg, 1902).
 1948 *Trochammina pacifica* Cushman var. *simplissima* Cushman & McCulloch: 76 (*nomen novum*).
 1956 *Trochammina simplissima* Cushman & McCulloch; Bandy: 198; pl. 29, figs 14a–c.
 1979 *Paratrochammina simplissima* (Cushman & McCulloch); Brönnimann: 10; figs 2,3,6A–J,8A–H (*q.v.* for full synonymy).

REMARKS. Millett's illustrated specimen, attributed to *H. nanum* Brady (*op.cit.* pl. 5, figs 9a–c; reproduced here as Figs 1.9a–c), is a sinistrally coiled specimen with 5 chambers in the final whorl. From the drawings it can be seen that the chambers of the final whorl are strongly compressed in an axial direction and the ultimate chamber is radially elongate. The intercameral sutures are well defined and the agglutinant of the spiral side appears to be distinctly coarser than that of the umbilical side. The aperture, which is an essential generic criterion, is only visible in edge view and its umbilical extension, if any, cannot be seen in the drawing of the umbilical side. We have searched the Millett Collection to find this figured specimen but the closest to it is a dextrally coiled individual (Figs 25–27), so it is possible that Millett's drawings could be reversed. Our figured specimen is undoubtedly *Paratrochammina simplissima* (Cushman & McCulloch). The single umbilical aperture is an elongate interiomarginal slit in the final septum, which extends from the surface of the first chamber of the final whorl onto that of the penultimate chamber. Its length is about 120 µm and it is lined by a weakly uplifted border of agglutinated fragments. The final whorl has 5 chambers, as in the original drawing, but the ultimate chamber, perhaps, is radially not as elongate as in Millett's figure. The test consists of 10 chambers, the coiling is rather tight and the axial depression (umbilicus) is therefore virtually closed. The radial sutures are well defined on both sides and the outline of the test is weakly lobate; the periphery, as seen in edge view, being compressed but still rounded. The spiral side is almost flat and the umbilical side slightly concave. As in Millett's illustrated specimen, ours is also more coarsely agglutinated on the spiral side than umbilically.

The marine, shallow water *P. simplissima* differs in all

pertinent features (size, chamber inflation and shape, aperture, etc.) from Brady's deep water species *Haplophragmium* (= *Trochammina*) *nanum* which was lectotypified, redescribed and illustrated by Brönnimann & Whittaker (1980: 177, figs 1–9). *P. simplissima* is highly variable in the overall shape and outline of the test (see Brönnimann, 1979: 14, figs 6A–J), however it is usually less compressed axially than Millett's specimens.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1141). Maximum diameter — 370 µm; minimum diameter — 280 µm; axial height (thickness) — 90 µm.

ENVIRONMENT. According to Millett (1899: 360), this species . . . 'is most abundant in Area 1'. It is a marginal marine species and significantly, was not listed where true brackish species such as *Acupeina triperforata*, *Ammoastuta salsa*, *Arenoparrella mexicana*, etc. were recorded.

Genus *TREMATOPHRAGMOIDES* Brönnimann & Keij, 1986

TYPE SPECIES. *Trematophragmoides bruneiensis* Brönnimann & Keij, 1986.

REMARKS. The genera *Haplophragmoides*, *Cribostrumoides*, and *Discammina* are all superficially similar to *Trematophragmoides*. *Trematophragmoides* Brönnimann & Keij is slightly evolute and planispiral with 3 apertures per chamber: a single primary equatorial interiomarginal aperture and one on each side of the chamber, umbilically situated on the suture and posteriorly directed. *Haplophragmoides* Cushman (1910) is also planispiral but has only one aperture per chamber. *Cribostrumoides* Cushman (1910) is usually involute, with streptospiral coiling initially, becoming planispiral in the adult whorls; the aperture is a equatorial, single areal slit (with lip) near the base of the septal face, becoming subdivided into a linear series of openings in gerontic forms. *Discammina* Lacroix (1932) is planispiral and slightly evolute, has a low interiomarginal equatorial aperture and is said to have an . . . 'interior divided by thin straight organic partitions, not corresponding to the original apertural face and not always reflected at the surface' (Loeblich & Tappan, 1987: 68).

Trematophragmoides bruneiensis Brönnimann & Keij, 1986 Figs 1.8, 28–30

1899 *Haplophragmium compressum* Goës; Millett: 359; pl. 5, figs 8a–c (non *Lituolina irregularis* var. *compressa* Goës, 1882).

1986 *Trematophragmoides bruneiensis* Brönnimann &

Keij: 16; pl. 1, fig. 1–10, pl. 2, figs 3–5, pl. 10, figs 1–3, text-fig. 1.

REMARKS. Brönnimann & Keij (1986) described from brackish waters of Brunei, NW Borneo, a planispiral agglutinated foraminifer with an interiomarginal and equatorial primary aperture and two secondary lateral apertures per chamber. The test shape is quite variable and the periphery, as seen in edge view, can be broadly rounded or compressed, almost subcarinate. Millett's roughly agglutinated species (1899, pl. 5, figs 8a–c; reproduced here as Fig. 1.8a–c), attributed by him to Goës' species *H. compressum*, shows two lateral openings and a single equatorial primary opening per chamber, and is undoubtedly a *Trematophragmoides*. Our SEM illustrations (Figs 28–30) show the same specimen as that drawn by Millett. As the early radial sutures are indistinct, the total number of chambers cannot be determined with certainty; the final whorl, however, contains 6 chambers. The lateral secondary apertures are well exhibited in Fig. 30 and the equatorial primary aperture in Fig. 29. Although the number of chambers in the final whorl is less than in the types of *T. bruneiensis*, other features agree well and there is no doubt that the two are one and the same.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1136). Maximum diameter — 470 µm; maximum thickness (final chamber) — 200 µm.

ENVIRONMENT. This species occurs only at Station 3. Millett (1899) does not offer any information about its association with other species, but from a study of his collection it can be seen to occur with '*Haplophragmoides*' *wilberti*. From this information, Station 3 must have been a brackish locality.

Genus *TROCHAMMINA* Parker & Jones, 1859

TYPE SPECIES. *Nautilus inflatus* Montagu, 1808.

Trochammina? *milleti* sp. nov. Figs 1.10, 22–24

1899 *Haplophragmium anceps* Brady; Millett: 361, pl. 5, figs 10a,b (non Brady, 1884).

DIAGNOSIS. Small conical, tightly-coiled *Trochammina?* with three large subglobular chambers in the final whorl.

NAME. In honour of Fortescue William Millett.

HOLOTYPE. BMNH no. 1955.11.1.1088. Illustrated in Figs 22, 23. This may be the specimen figured by Millett (1899, pl. 5, figs 10a,b; reproduced here as Figs 1.10a,b). From Station 12, Area 1.

DESCRIPTION (HOLOTYPE). Test free, dextrally coiled conical trochospire with pointed initial portion. Final volution

Figs 45–47 *Ammotium directum* (Cushman & Brönnimann). Figs 45, 46, Detail of aperture (×975 and ×280, respectively). BMNH no. 1955.11.1.1119; Fig. 47, Side view (×160). BMNH no. ZF 4999, mangrove sediments, Brönnimann sample 93, Acupe, Brazil

Figs 48, 49, 51, 52 *Ammotium subdirectum* Warren. Figs 48, 49, Side and edge views (×85). BMNH no. ZF 5000; Figs 51, 52, Side and oblique-apertural views (×85 and 125, respectively). BMNH no. ZF 5001. Both from mangrove sediments, Brönnimann sample 93, Acupe, Brazil.

Figs 50, 53 *Ammotium pseudocassis* (Cushman & Brönnimann). Side view (×160) and separate specimen in clearing oil (×265). Brönnimann Collection, mangrove sediments, Guaratiba, Brazil.

Fig. 54 *Ammotium morenoi* (Acosta). Side view (×205). Brönnimann Collection, mangrove sediments, Guaratiba, Brazil.

Fig. 55 *Ammotium distinctum* (Cushman & Brönnimann). Side view in clearing oil (×330). Brönnimann Collection, sample 145, from Acupe, Brazil.

All from Millett Collection, Malay Archipelago, except where stated.



triseriate, consisting of large subglobular chambers, somewhat compressed in axial direction, making up major part of the test. Coiling tight and axial depression (umbilicus) closed. Sutures well defined. Single interiomarginal aperture a small arch resting with its slightly upturned border completely on surface of first chamber of final whorl. Agglutinant rather coarse.

DIMENSIONS (HOLOTYPE). Height of test — 160 µm; width (umbilical diameter) — 150 µm.

REMARKS. Millett (*op.cit.*, pl. 5., figs 10a,b) attributed this small, rather fragile, conical form, to *Haplophragmoides anceps* Brady. The aperture is a broadly rounded interiomarginal arch, sitting with its border completely on the final whorl and therefore the species should belong to *Trochammina* (see Brönnimann *et al.*, 1983). Fig. 23 illustrates a typical specimen from the Millett Collection but there are extremes (Paratype BMNH no. 1955.11.1.1088; Fig. 24) where the height of the trochospire and the umbilical diameter are about the same or the former even appears to be slightly larger. In 1983, Brönnimann *et al.* held great store by the fact that in the Trochamminacea the umbilical diameter was invariably greater than the length of the axis of coiling (height of the trochospire), whereas in the Ataxophragmacea the reverse was true. This is the first time we have found a species, and apparently a single population, at the borderline of the two groups. For this reason we have only tentatively placed this interesting species in *Trochammina*.

The true *H. anceps* Brady, 1884 is the type species of *Globotextularia* Eimer & Fickert, 1899. This is a robust, deep water form, much larger than Millett's species, with a very high, often irregular coil, an open umbilicus and larger aperture.

ENVIRONMENT. According to Millett (1899: 361), . . . 'specimens [of "*H. anceps*"] are numerous and well distributed'. They are found at stations 5, 11, 12 (Area 1) and 27, 28 (Area 2). It is associated with the agglutinating foraminifera *Ammobaculites exiguus* at stations 12 and 27 and rare *Acupeina triperforata*/*Arenoparrella mexicana* at Station 5. The former is found in both marginal marine and brackish localities, whereas the latter are true brackish forms. It is therefore not known for certain whether *T.?* *milleti* is a marine or a brackish species.

Genus **TRUNCULOCAVUS** gen. nov.

TYPE SPECIES. *Trunculocavus durrandi* sp. nov.

DIAGNOSIS. Test free, initially biserial, then abruptly uniserial. Biserial chambers subglobular, uniserial chambers with circular transverse section. Wall agglutinated, of Trochamminina-type. Aperture single, terminal, circular and large, devoid of everted border.

NAME. Derived from the Latin: *cavus*, a hole or hollow, and *trunculus*, tip or end.

REMARKS. Our new genus has the basic morphology of *Bigenenerina* d'Orbigny, 1826 (type species *B. nodosaria* d'Orbigny, 1826), but differs in the large circular aperture of the final chamber of the uniserial stage, devoid of a border structure. In contrast, the terminal aperture of *B. nodosaria* is a small central porus with everted border. According to Loeblich & Tappan (1987: 172), *Bigenenerina* also has a perfor-

ate ('canaliculate') wall, whereas *Trunculocavus* has a Trochamminina-type wall.

In the Millett material, there are well-preserved specimens of *Trunculocavus durrandi* showing an organic structure within the large rounded aperture. This structure is different from the inner organic sheet (inner organic lining in the sense of Bender, 1989: 278), which occurs along the inside of the wall of the Trochamminina, because it is independent of the agglutinated-organic wall proper. It is suggested that it represents the epidermal layer of the protoplasmic body of the foraminifer. Therefore, we must distinguish between this type of organic structure, as part of the protoplast, and the inner organic sheet which covers the inside of the agglutinated wall of the Trochamminina-type test (see Brönnimann & Whittaker, 1988), which, although has also been produced by the protoplast, is not directly part of it.

This organic structure, or the epidermal layer of the protoplasmic body, occurs inside the terminal aperture of the test, either as a large rounded opening limited by a thickened border (Fig. 7), or it closes the aperture of the test completely and reveals 6 small perforations with tube-like extensions (Fig. 1) along the apertural periphery. This organic structure does not have a counterpart in the agglutinated-organic phase of the wall, another reason for separating it nomenclatorally from the inner organic sheet. In fossil specimens, the epidermal layer of the protoplast will naturally be absent, so it could not be considered taxonomically. At present, therefore, it has no standing in the systematic treatment of these agglutinated foraminifera, which is based on test features alone. It should, however, be remembered that this situation would have to be modified once it becomes possible to take into consideration the features of the living organism.

In a paper by Petrucci *et al.* (1983: 72–75), there is a taxonomic appendix by Medioli, Scott & Petrucci. In this appendix a new species, *Polysaccammina hyperhalina*, is introduced which is of interest here because it shows organic features similar to those described for *T. durrandi*. *P. hyperhalina* has a large circular terminal aperture with an irregularly finished border, devoid of particular border structures. Medioli *et al.* (1983: 72, pl. 21, figs 2,3,6,8) described the aperture as invaginated . . . 'to form an inner, backward pointing funnel'. Their pl. 1, figs 1a,2a show the large, rounded aperture is closed on the inside, as in *T. durrandi*, by an organic structure having in its centre a small circular porus with everted border. Also, as in *T. durrandi*, this small opening appears to be a different from the aperture of the test and that it represents the epidermal layer of the protoplast, with features which have no counterpart in those of the test wall and which is different from the inner organic lining.

Trunculocavus durrandi sp. nov.

Figs 2.1,3–8

1900 *Bigenenerina digitata* d'Orbigny var. Millett: 6, pl. 1, figs 1a,b (*non Bigenerina (Gemmulina) digitata* d'Orbigny, 1826).

DIAGNOSIS. As for genus; *Trunculocavus* is presently monotypic.

NAME. In honour of A. Durrand FRMS, the collector of the Malay Archipelago foraminifera described by Millett.

HOLOTYPE. BMNH no. 1955.11.1.187. Illustrated in Figs 3,4. From Station 9, Area 1.

DESCRIPTION (HOLOTYPE). Test free, small and elongate; ini-

tially a subglobular protoconch, followed by 4 pairs of subglobular, biserial chambers, then abruptly uniserial with 3 cylindrical chambers. Aperture large, terminal and central without everted border; the inner organic sheet closing the aperture, however, develops around its circumference, 6 minute pores with tubular borders. Agglutinated wall of granular, but overall smooth appearance. Tubular organic pores have no counterpart in agglutinated phase.

DIMENSIONS (HOLOTYPE). Height of test — 270 μm ; maximum width of test — 75 μm ; diameter of aperture — 35 μm ; diameters of tubular pores around circumference of aperture — 4–5 μm .

PARATYPES. Two paratypes (BMNH nos. 1955.11.1.188, 189) are illustrated in Figs 5–8. In side view, they are as the holotype with a short biserial stage followed by the uniserial stage composed of 2 or 3 cylindrical chambers. Paratype (BMNH no. 1955.11.1.188; Figs 6–8) shows an aperture where the inner organic sheet does not close the opening. The sheet itself has an opening, bordered by a thickened rim, which is virtually of the same diameter as the rounded terminal aperture of the agglutinated phase; there are no minute pores as in the holotype.

DIMENSIONS (PARATYPES). (BMNH no. 1955.11.1.188) Height of test — 230 μm ; maximum width — 90 μm ; diameter of aperture — 40 μm .

(BMNH no. 1955.11.1.189) Height of test — 240 μm ; maximum width 75 μm .

REMARKS. Millett's actual figured specimen (1900, pl. 1, figs 1a, b; reproduced here as Figs 2.1a, b) could not be recognised with certainty. Millett's drawing, however, shows a specimen with a rather indistinct biserial initial portion of 4 or 5 pairs of chambers, then a 4 or 5-chambered uniserial stage; the uniserial chambers are cylindrical and the large terminal rounded aperture is devoid of an everted border.

ENVIRONMENT. According to Millett (1900: 6), this species is . . . 'confined to Station 9, and the examples, although minute, are moderately abundant'. From the same locality Millett (1899: 358, 359) also found *Acupeina triperforata*, *Arenoparrella mexicana*, '*Ammobaculites*' *exiguus*, *Ammoastuta salsa* and *Ammotium* spp., all brackish, mangrove sediment-dwelling species. It is therefore assumed that *T. durrandi* also lives in a brackish habitat.

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Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (= Toxoglossa) (Gastropoda)

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SYNOPSIS. A survey of the anterior alimentary system of species from all the higher taxa of the highly diverse gastropod superfamily Conoidea (including the Turridae, Terebridae, and Conidae) has revealed a great variety of foregut structure. A series of anatomical characters of the rhynchodeum, proboscis, buccal mass, radular apparatus and foregut glands has been defined and their distribution established amongst the various conoidean families and sub-families. Twelve major types of foregut structure were recognised, which ranged from gastropods with a full set of foregut organs and glands to others in which most of the structures including the radula, venom gland and proboscis are absent. A set of these anatomical characters together with a few shell characters were used in a cladistic analysis attempting to determine relationships amongst the conoidean higher taxa. A classification incorporating the new anatomical data and based partly upon the phylogenetic analysis recognises 6 families and 13 subfamilies of Conoidea. New data suggest that the Pervicaciinae and Terebrinae share a common ancestor and there is little evidence to justify familial separation of the Coninae. Some major foregut structures seem to have evolved independently in different clades. Thus, hollow ‘hypodermic’ radular teeth have been derived independently in a least five clades; the radular caecum and rhynchodeal introvert have evolved independently in two clades. Several clades also show loss of major foregut structures such as the proboscis, venom gland and radular apparatus. Finally, the 378 genera of Recent ‘Turridae’ are placed into the higher taxa recognised in the proposed classification.

INTRODUCTION

The prosobranch gastropod superfamily Conoidea (=Toxoglossa), which includes the families Turridae, Conidae, Pervicaciidae and Terebridae, is extremely diverse, with as many as 679 genera and 10,000 living and fossil species claimed for the Turridae alone (Bouchet, 1990) and *Conus* with around 500 living species, is considered to be the most diverse genus of marine animal (Kohn, 1990). Current classifications of taxa within the Conoidea are based almost entirely upon shell

characters, or upon a combination of shell and radular characters (Turridae–Powell, 1966; McLean 1971; Kilburn, 1983, 1985, 1986, 1988; Terebridae–Bratcher & Cernohorsky, 1987). The Turridae are the most morphologically disparate of the four families with seventeen subfamilies in current use. However, most of these subfamilies are rather poorly defined. Despite the biological interest in the venom apparatus of the group, little is known of the relationships of the Conoidea to other gastropods, of relationships between the families of the Conoidea or of relationships within the constituent families.

The Conoidea are considered to be monophyletic, because the families share the common apomorphy of a venom apparatus consisting of the venom gland and muscular bulb. This is thought to have been lost in some taxa, such as some highly-derived members of the Daphnellinae and Terebridae (Kantor & Sysoev 1989; Taylor, 1990) and all Strictispirinae.

Compared with the number of living species and the attention paid to the description of shells, particularly of Conidae, there have been very few anatomical studies of Conoidea. However, recently, a much wider range of species from the Turridae, Terebridae and Pervicaciidae (Sysoev & Kantor 1987, 1988, 1989; Kantor & Sysoev, 1989; Miller, 1989, 1990; Kantor, 1990; Taylor, 1990) have been investigated anatomically. These studies illustrate the great variety of foregut anatomy, particularly within the Turridae and Terebridae. By comparison, the Conidae appear to have a relatively uniform foregut anatomy (Marsh, 1971; Miller, 1989), although they have been surprisingly little studied.

Until recently, attempts to use anatomical characters in determining relationships amongst conoideans were constrained either by the limited range of taxa that had been studied or by the small number of characters used. For example, an evolutionary scenario for the Conoidea based upon characters of foregut anatomy was proposed by Sheridan *et al.* (1973), but species were studied from only three out of the seventeen turrid subfamilies. Additionally, Shimek & Kohn (1981) used only radular characters to produce a cladistic analysis of a wider range turrid taxa.

Another problem in comparing the different taxa studied within the Conoidea, is that the nomenclature for the different anatomical structures is inconsistent and very confused. This has hampered the recognition of homologous structures that may be shared between the different taxa.

In this paper we attempt a comparative review of the anatomy and functional morphology of the conoidean foregut. We have attempted to examine species from all the currently-recognised subfamilies of Turridae, many species of Terebridae, Pervicaciidae and a few species of *Conus*. Additionally, we have incorporated previously published studies into our review and attempted to standardize the nomenclature of the anatomical structures.

The overall objectives of the study are, firstly, to evaluate the use of characters of foregut anatomy in determining relationships among the Conoidea and secondly, to propose a new classification of conoidean higher taxa which incorporates these anatomical characters. Foregut anatomy was chosen as the focus for this study, because a few previous studies (Sheridan *et al.* 1973; Kantor, 1990) had drawn attention to the diversity and complexity of the digestive system. As far as is known, other organ systems are similar to other neogastropods.

MATERIAL AND METHODS

The material on which this study is based consists mainly of longitudinal serial sections of the foreguts of a wide range of gastropods from all of the currently recognised subfamilies of Turridae, many Terebridae and Pervicaciidae and a few species of Conidae (Table 1). Dissections were also made of most of these species. Also indicated in Table 1 are species for which we have used previously published anatomical

descriptions in our analysis. Additionally, radular preparations were made from a range of other species.

Critical-point dried preparations for scanning electron microscopy were made of some anatomical structures and some small species (methods in Taylor & Miller, 1989). Radula preparations for both light and scanning microscopy were made by standard methods.

FOREGUT ANATOMY

A generalized diagram of the conoidean foregut (Fig. 1) shows the relative positions of the major structures.

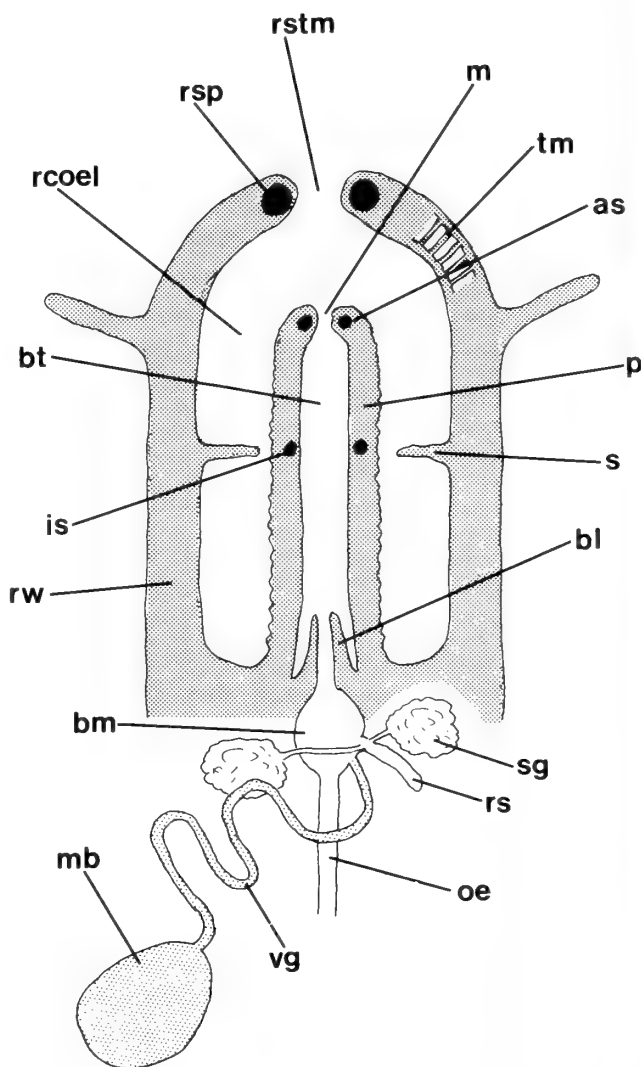


Fig. 1 Composite diagram of the foregut of a hypothetical conoidean gastropod showing the location of the major structures discussed in the text. No single gastropod possesses all these features. Abbreviations: as, anterior sphincter of buccal tube; bl, buccal lips; bm, buccal mass; bt, buccal tube; is, intermediate sphincter of buccal tube; m, mouth; mb, muscular bulb; oe, oesophagus; p, proboscis; rcoel, rhynchocoel; rs, radular sac; rsp, rhynchostomal sphincter; rstm, rhynchostome; rw, rhynchodeal wall; s, septum; sg, salivary gland; tm, transverse muscles of rhynchodeal wall (shown in part only); vg, venom gland.

Table 1. List of species examined in this study. The classification in the list is traditional and follows Powell (1966), McLean (1971) and Kilburn (1983–89). A new classification is given at the end of this paper. The prefix 'a' denotes species that were studied anatomically and the prefix 'r' denotes species for which only the radula was examined. In most cases, animals were both dissected and serial sections made of the anterior alimentary systems.

Pseudomelatomininae

- a*Pseudomelatoma penicillata* (Carpenter, 1864). Punta San Bartolome, Mexico.
a*Hormospira maculosa* (Sowerby, 1834). Sonora, Mexico

Drilliainae

- a*Clavus unizonalis* (Lamarck, 1822). Lizard I., Queensland, Australia.
a*Clavus* sp. (undescribed species). Guam.
a*Splendrilla chathamensis* Sysoev & Kantor, 1989. Chatham Rise, South Pacific.
r*Drillia cydia* (Bartsch, 1943). British Virgin Islands.
r*Drillia rosacea* (Reeve, 1845). West Africa.
r*Imaclava unimaculata* (Sowerby, 1834). Baja California, Mexico.
r*Spirotropis monterosatoi* (Locard, 1897). East Atlantic.
r*Crassopleura maravignae* (Bivona, 1838). Naples, Italy.

Clavatulininae

- a*Toxoclonella tumida* (Sowerby, 1870). South Africa.
a*Clionella sinuata* (Born, 1778). Oudekraal, South Africa.
a*Clavatula caerulea* (Weinkauff, 1875). Sierra Leone, West Africa.
a*Clavatula muricata* (Lamarck, 1822). Dakar, Senegal.

Turrinae

- r*Lophiotoma acuta* (Perry, 1811). Lizard I., Queensland, Australia.
a*Gemmula deshayesi* (Dumet, 1839). Hong Kong.
r*Gemmula kieneri* (Dumet, 1840). Hong Kong.
a*Lophiotoma leucotropis* (Adams & Reeve, 1850). Hong Kong.
a*Polystira albida* (Perry, 1811). Caribbean. Data from Leviten (1970).

Cochlespirinae

- a*Turricula javana* (Linnaeus, 1767). Hong Kong.
a*Turricula nelliae spurius* (Hedley, 1922). Hong Kong.
a*Aforia abyssalis* Sysoev & Kantor, 1987. North-East Pacific.
a*Aforia leptia* (Watson, 1881). South Pacific, nr New Zealand.
a*Aforia inoperculata* Sysoev & Kantor, 1988. North-East Pacific.
a*Alrenosyrinx hypomela* (Dall, 1889). East Atlantic.
a*Antiplanes sanctioannis* (Smith, 1875). Okhotsk Sea.
r*Antiplanes vinosa* (Dall, 1874). Sakhalin Bay, Okhotsk Sea.

Crassispirinae

- r*Austrodrillia angasi* (Crosse, 1863). Sydney, Australia.
a*Funa latisinuata* (Smith, 1877). Hong Kong.
a*Inquisitor* spp. Indian Ocean.
a*Vexitomina garrardi* (Laseron, 1954). Sydney, Australia.
r*Ptychobela griffithi* (Gray, 1834). Karachi.

Strictispirinae

- a*Strictispira paxillus* (Reeve, 1845). British Virgin Islands.
r*Strictispira stillmani* Shasky, 1971. Panama.
r*Cleospira ochsneri* (Hertlein & Strong, 1849). Galapagos Islands.

Zonulispirinae

- a*Pilsbryspira nympha* (Pilsbry & Lowe, 1932). Sonora, Mexico.

Borsoniinae including **Mitrolumninae** (fide Kilburn, 1986)

- a*Lovellona atramentosa* (Reeve, 1849). Guam.
a*Anarithma metula* (Hinds, 1843). Indian Ocean.
a*Borsonia ochraea* Thiele, 1925. Indian Ocean, nr Zanzibar 740m.
a*Micanthapex parengonius* (Dell, 1956). South Pacific, nr New Zealand.
a*Tomopleura reevei* (C.B. Adams, 1850). Indian Ocean.
a*Suavodrillia kennicotti* (Dall, 1871). Japan Sea.
a*Tropidoturris anaglypta* Kilburn 1986. Southern Indian Ocean.
a*Tropidoturris fossata notialis* Kilburn, 1986. South Africa.
a*Ophioidermella inermis* (Hinds, 1843). Bremerton, Washington.
a*Ophioidermella ogurana* (Yokoyama, 1922). Japan Sea.

Clathurellinae

- a*Glyphostoma candida* (Hinds, 1843). Sonora, Mexico.

Mangeliinae

- a*Mangelia brachystoma* (Philippi, 1844). Galway, Ireland.
a*Mangelia nebula* (Montagu, 1803). Galway, Ireland. Also data from Sheridan *et al.* (1973) & Delaunoy & Sheridan (1989).
a*Mangelia powisiana* (Dautzenberg, 1887). Plymouth, England.
a*Eucithara stromboides* (Reeve, 1846). Guam.
a*Hemilienardia malleti* (Recluz, 1852). Guam.
a*Paramontana cf. rufozonata* (Angas, 1877). Rottnest I., Western Australia.

Oenopotinae

- a*Oenopota levidensis* (Dall, 1919). Washington. Data from Shimek (1975)
r*Propebela rugulata* (Moller, 1866). White Sea.

Daphnellinae

- a*Comarmondia gracilis* (Montagu, 1803). Brittany, France. Data from Sheridan *et al.* (1973)
a*Daphnella reeveana* (Deshayes, 1863). Guam.
a*Gymnobela emertoni* (Verrill & Smith, 1884). Eastern Atlantic Ocean.
a*Teretioopsis levicarinatus* Kantor & Sysoev, 1989. Eastern Atlantic Ocean.
a*Abyssobela atoxica* Kantor & Sysoev, 1986. Northern Pacific Ocean.
a*Gymnobela latistriata* Kantor & Sysoev, 1986. Northern Pacific Ocean.
a*Gymnobela oculifera* Kantor & Sysoev, 1986. Northern Pacific Ocean.
a*Pontiothauma abyssicola* Smith, 1895. Indian Ocean. Data from Pace (1901).
a*Pontiothauma mirabile* Smith, 1895. Indian Ocean. Data from Pace (1901)

Conorbinae

- a*Benthofascis biconica* (Hedley, 1903). Sydney, Australia.
a*Genota mitraeformis* (Woods, 1828). West Africa.
a*Genota nicklesi* Knudsen, 1952. West Africa.

Thatcheriinae

- a*Thatcheria mirabilis* Angas, 1877. North Western Australia.

Taraniinae

- a*Taranis moerchi* (Malm, 1861). Sweden.

Conidae

- a*Conus flavidus* Lamarck, 1810. Queensland, Australia, Data from Marsh (1971)
a*Conus ventricosus* Gmelin, 1791. Tunisia.

Pervicaciidae

- a*Pervicacia capensis* (Smith, 1873). South Africa.
a*Pervicacia kieneri* (Deshayes, 1859) Albany, Western Australia.
a*Pervicacia tristis* (Deshayes, 1859). New Zealand.
a*Duplicaria colorata* Bratcher, 1988. Western Australia.
a*Duplicaria duplicata* (Linnaeus, 1758). Kenya.
a*Duplicaria spectabilis* (Hinds, 1844). Hong Kong.
a'*Terebra*' *nassoides* Hinds, 1844. Oman.

Terebridae

- a*Hastula aciculina* (Lamarck, 1822). Ghana.
a*Hastula bacillus* (Deshayes, 1859). Phuket, Thailand.
a*Terebra affinis* Gray, 1834. Guam.
a*Terebra babylonica* Lamarck, 1822. Guam.
a*Terebra gouldi* Deshayes, 1857. Hawaii.
a*Terebra maculata* Linnaeus, 1758. Guam.
a*Terebra subulata* Linnaeus, 1767. Maldives.

Characters of the rhynchocoel

In all toxoglossans there is a permanent cavity in the anterior part of the body called the rhynchodeal cavity or rhynchocoel (Fig. 1). It contains the proboscis and is maintained even when the proboscis is extended. The rhynchodeal cavity opens to the exterior via the rhynchostome, which is situated at the ventral margin of the head. The walls of the rhynchocoel (rhynchodeum) are usually thick and muscular.

Rhynchostomal sphincter

This is an annular, muscular sphincter which encircles the mouth of the rhynchocoel (Fig. 1). It is present in most species of Turridae, Terebridae, Pervicaciidae and Conidae, but absent in the turrids *Clavatula diadema* and *Tomopleura violacea* and the pervicaciids *Pervicacia tristis*, '*Terebra*' *nasoides*, and '*T.*' *capensis*. In these latter pervicaciids and some turrids without a prominent sphincter, for example *Tomopleura*, the anterior part of the rhynchodeum is very muscular.

Position of rhynchostomal sphincter

In the normal condition, the sphincter is usually situated around the rhynchostome, but in some turrids (for example in *Glyphostoma*, *Borsonia*, *Lophiotoma*, *Pontiothauma* and *Thatcheria*) it is situated more posteriorly. In *Ophiidermella inermis* (but not *O. ogurana*) and *Suavodrillia kennicotti* the moderately large, posteriorly situated, rhynchostomal sphincter is probably able to evert, forming a sort of 'rhynchostomal introvert' but situated in the middle part of the rhynchocoel (Fig. 2). The ability to evert is indicated by the presence of a well-developed layer of longitudinal muscles underlying the epithelium and by the existence of free space between the sphincter and the longitudinal muscle layers. This structure may demonstrate the possible origin of the true rhynchodeal introvert (see below) or alternatively be an autapomorphy for the species.

Rostrum

In some fish-feeding species of *Conus*, the anterior part of the rhynchocoel is elastic and can be greatly extended to accommodate large food items during preliminary digestion. This extensible feature, known as the rostrum, cannot be inverted into the rhynchocoel.

Rhynchodeal introvert (= labial tube or pseudoproboscis)

In this structure, the rhynchostomal lips are mobile and can be retracted into the rhynchocoel by infolding, or extended as a tube (Figs 3 & 4). The introvert is found in nearly all the species which we and others have studied from the turrid sub-family Daphnellinae, e.g. *Philbertia linearis*, *P. leufroyi*, *P. gracilis*, *Cenodagreutes*, *Daphnella reeveana* (Smith, 1967; Sheridan *et al.*, 1973; unpublished observations), in *Hemilienardia malleti* (Mangeliinae) and in all Terebridae and Pervicaciidae (Miller, 1975, 1980; Taylor, 1990). We have not seen an introvert in any other subfamily of Turridae (except perhaps for *Ophiidermella*, see above), or in the Conidae. In species of Daphnellinae the introvert is fairly short, but in some terebrids, for example *Terebra maculata*, the introvert

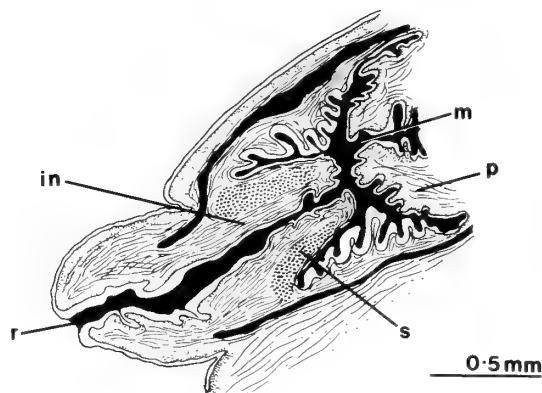


Fig. 2 *Ophiidermella inermis*; longitudinal section of the anterior rhynchodeum showing the posteriorly-situated, rhynchostomal sphincter located on an introvert-like structure. Abbreviations: in, introvert; m, mouth; p, proboscis; r, rhynchostome; s, sphincter.

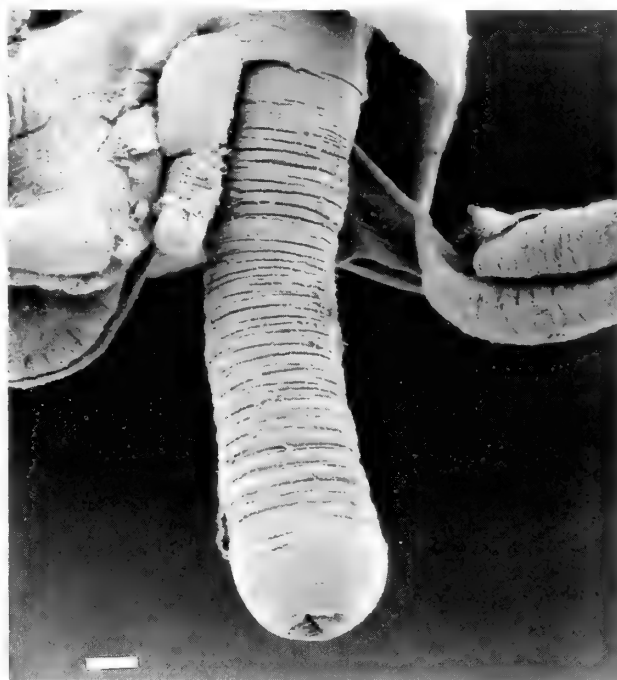


Fig. 3 *Hemilienardia malleti*; extended rhynchodeal introvert, forming a pseudoproboscis in a relaxed, critical-point dried specimen. Scale bar = 100 µm.

is very long, and when retracted, lies coiled in the rhynchocoel (Miller, 1970).

In those animals possessing a rhynchodeal introvert, the outer and inner walls are joined by radial muscles (Fig. 5). In Turridae, the possession of an introvert is associated with a reduction in size or complete loss of the proboscis. However, within the Terebridae, even those species with a well-developed proboscis possess an introvert.

Epithelium of the rhynchodeum

In some Turridae, there is a distinct division in the character of the epithelium lining the inner wall of the rhynchocoel. In the anterior part of the cavity the epithelial cells are high and

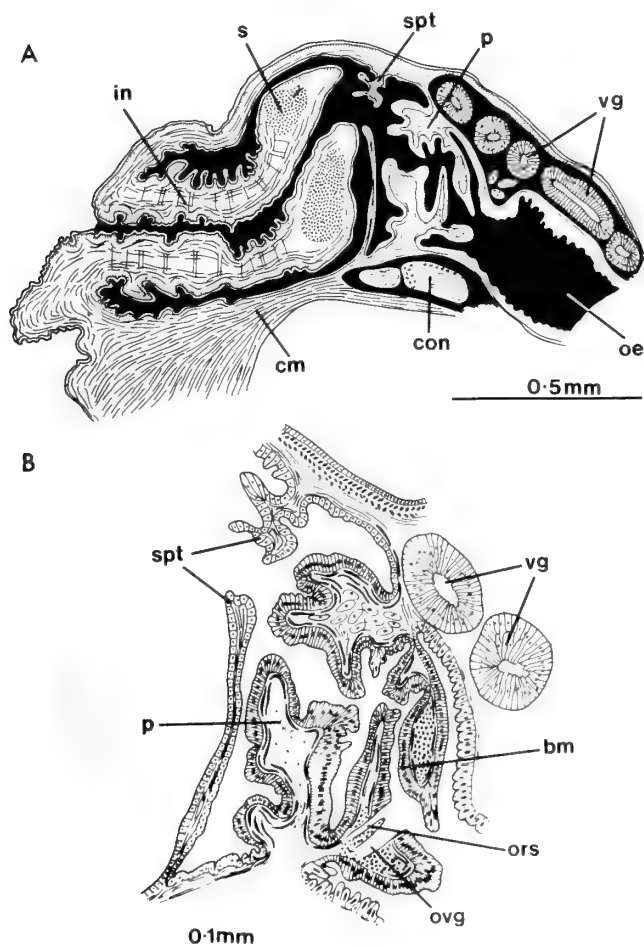


Fig. 4 *Daphnella reeveana*; A, longitudinal section through the foregut; B, Enlargement of the mouth area showing the short proboscis lying behind the septum. Abbreviations: bm, buccal mass; cm, columellar muscle; con, circum-oral nerve ring; in, rhynchodeal introvert; oe, oesophagus; ors, opening of radular sac; ovg, opening of venom gland; p, proboscis; s, rhynchostomal sphincter; spt, septum; vg, venom gland.

glandular (Fig. 6C), but in the posterior half the epithelium is low, cuticularized and similar in morphology to that of the outer surface of the proboscis. This feature indicates that the posterior part of the rhynchodeum can be extended outwards when the proboscis is protruded through the rhynchostome. We have observed this condition of the rhynchocoel epithelium in *Clavatula*, and *Clionella* (Clavatulinæ), *Vexitomina* (Crassispirinae), *Turricula nelliæ spurius* (Cochlespirinae), *Pilsbryspira nympha* (Zonulispirinae), and *Anarithma metula* (Borsoniinae).

In 'lower' turrids, excepting *Vexitomina*, this feature seems to be associated with those species in which the buccal mass lies in a distal position within the proboscis (see below). Its presence may be connected with the mechanism by which the buccal mass is everted from the proboscis tip.

Septum in rhynchodeum

A thin, slightly muscular septum, pierced by a circular orifice, and dividing the rhynchodeal cavity into two parts is known in *Daphnella reeveana* (Fig. 4), *Philbertia purpurea* (Sheridan *et al.*, 1973) and *Terebra subulata* (Taylor, 1990). The probos-

cis, when withdrawn, lies behind the septum, with the retracted introvert lying to the anterior. A probably homologous septum is also found at the extreme posterior and ventral end of the rhynchocoel in *Thatcheria* and *Pontiothauma* (Pace, 1901). A thin septum is also found in the posterior part of the rhynchocoel in *Pervicacia tristis* (not reported by Rudman (1969)) and in *Duplicaria kieneri* (Taylor, unpublished).

The function of the septum is unknown, but it appears better developed in species with a long proboscis and where the proboscis withdraws behind the septum.

Accessory proboscis structure

This is an extensible muscular structure which arises from the left hand wall of the rhynchocoel. It has been found only a few species of Terebridae and Pervicaciidae. It is long and branched in *Hastula bacillus* (Taylor & Miller, 1990), shorter and club-like in *Terebra affinis* (Miller, 1971), '*Hastula*' *colorata* and *D. kieneri* and a curved, club-shape in *Terebra imitatrix* (Auffenberg & Lee, 1988). In *H. bacillus* the accessory proboscis is covered in possible chemosensory structures (Taylor & Miller (1990)).

Snout gland

This is a subspherical gland which opens into the right-hand posterior end of the rhynchocoel in a number of *Conus* species (Marsh, 1971). The gland consists of folded glandular epithelium (Fig. 7) and is surrounded by a muscular sheath of circular muscles. From histochemical tests, Marsh (1971) concluded that the gland secretes mucus. The gland has been reported in 18 species of *Conus*, all but one of which are known to be vermivorous (Marsh, 1971).

The proboscis and its structures

An extensible proboscis arising from the posterior of the rhynchocoel is present in the Drilliinae (formerly Clavinae; ICZN decision pending on further name change to Clavusiinae) and all the radulate turrids examined, excepting *Gymnobela emertoni*, where the radula is vestigial. A proboscis is present in all species of *Conus*, in *Hastula*, and in other radulate Terebridae, such as *T. subulata*, and *T. babylonica* (Taylor, 1990). The distal opening to the proboscis forms the true mouth as in all probosciferous gastropods. Shimek (1975) referred to the opening of the buccal cavity as being the true mouth.

A proboscis is absent in the radula-less Turridae such as *Teretopsis*, *Taranis* (Kantor & Sysoev, 1989), *Philbertia leufroyi boothi*, *P. linearis* (Smith, 1967, Sheridan *et al.*, 1973) and the radulate *Gymnobela emertoni*. A proboscis is also absent in species of *Duplicaria* and *Pervicacia*, which are radulate forms of the Pervicaciidae (Taylor, 1990), and in the many species of Terebridae which lack a radula, such as *Terebra maculata*, *T. gouldi*, *T. dimidiata*, and *T. affinis* (Miller, 1970, 1975; Taylor, 1990).

In *Duplicaria spectabilis* and *Gymnobela emertoni* we have observed a low cylinder of muscular tissue surrounding the opening to the buccal cavity (Fig. 8) (Taylor (1990, Fig. 2). We think that this may represent the remnant of a much reduced proboscis. A similar reduced structure found in *Cenodageutes* spp. and *Philbertia linearis*, was described by Smith (1976) as the muscular sheath.

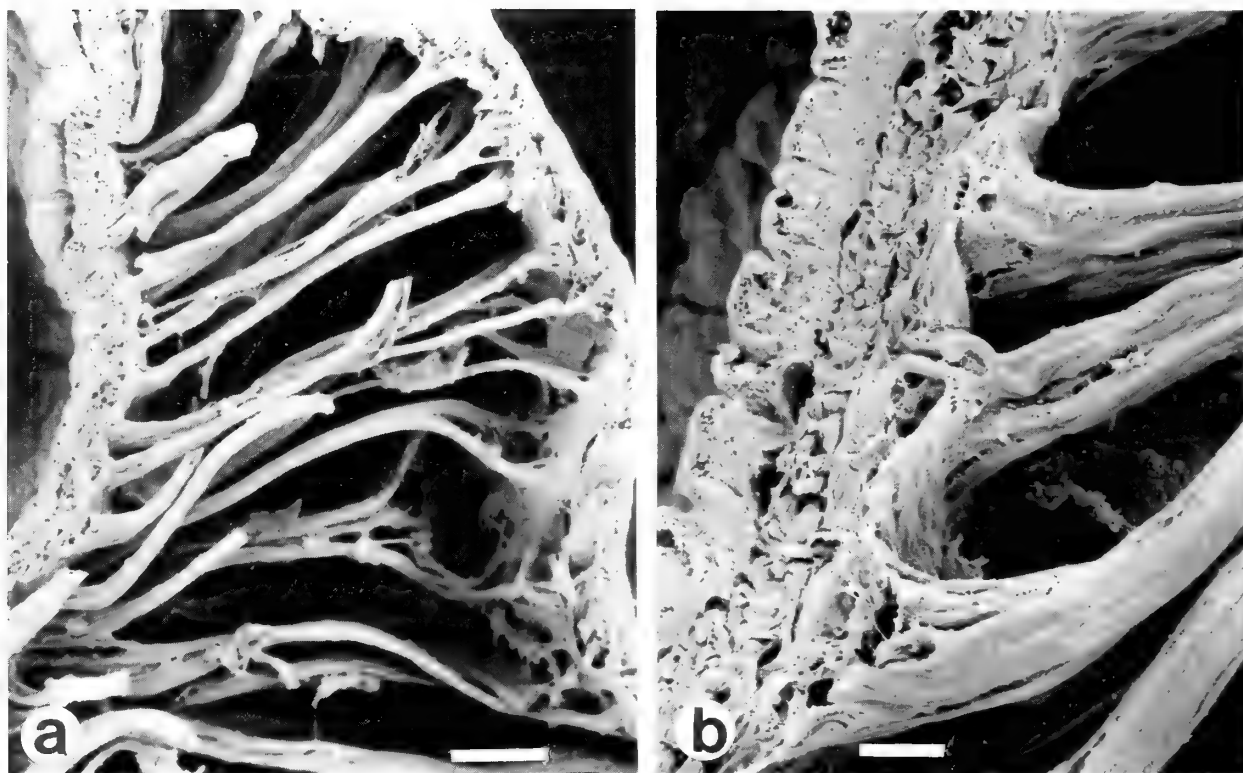


Fig. 5 *Duplicaria spectabilis*; relaxed, critical-point dried specimen. A, Section of the rhynchodeal wall showing the transverse muscles joining the inner and outer walls. Scale bar = 100 μ m. B, Detail of junction of transverse muscles joining the inner wall of the rhynchodaeum. Scale bar = 20 μ m.

Buccal tube

The buccal tube is that portion of the alimentary canal lying between the buccal cavity and the true mouth, which is situated at the distal end of the proboscis. The buccal tube is present in all toxoglossans with a proboscis and is absent only in those species where that organ is lost. It is very short in *Strictispira paxillus* where the buccal mass lies at the extreme anterior end of the proboscis.

In the Mangeliinae the epithelium of the buccal tube is very thin (Fig. 9), but much thicker in species of other subfamilies such as the Drilliinae and Clavatulinae (Fig. 6). Shimek (1975) referred to the buccal lips (see below) as the buccal tube, and he called the true buccal tube, the inner proboscis wall.

Buccal tube sphincters

In most toxoglossans, one or more annular sphincters may be found in various positions within the proboscis.

a) Distal sphincter(s)

In most species with a proboscis, there is a distal sphincter around the true mouth. Frequently, there is a second sphincter also near the proboscis tip, but located just to the posterior of the first (Fig. 6). In 'lower' turrids such as the Drilliinae Cochlespirinae and Clavatulinae, the sphincter(s) grip the solid, radular teeth whilst they are held at the proboscis tip (Sysoev & Kantor, 1989; Kantor & Taylor, 1991).

b) Intermediate sphincter

A small muscular sphincter, situated about half way along the length of the proboscis is found in *Splendrillia* (Kantor & Sysoev, 1989, fig. 3c). Species of *Conus* also have a sphincter situated some distance posterior to the proboscis tip (Greene & Kohn, 1989) which we classify as an intermediate sphincter.

c) Basal sphincter

A sphincter located near the base of the proboscis has been described for *Mangelia nebula* (Sheridan *et al.*, 1973). Recently, Delaunois & Sheridan (1989) have illustrated a section through the buccal area of *M. nebula*, showing a single radular tooth held in the buccal tube. The tooth is gripped at the anterior end by the buccal tube introvert (see below), and the posterior end by the basal sphincter (Fig. 9).

Buccal tube introvert

This is a muscular, flap-like structure found towards the distal end of the buccal tube of *Mangelia nebula* (Fig. 9) and called a valve (valvule) by Sheridan *et al.* (1973). *Eucithara stromboides* has a longer, but apparently homologous structure (Fig. 10). Delaunois & Sheridan (1989) showed that one of the functions of this structure is to grip the radular tooth in the buccal tube, but in *Eucithara* where the structure is very long (Fig. 10), it may possibly be used to transport teeth to the proboscis tip.

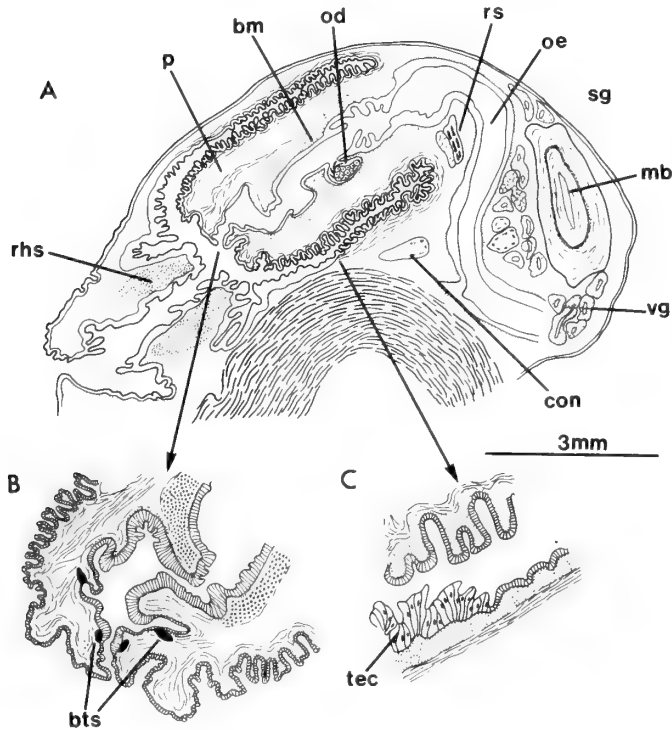


Fig. 6 *Clionella sinuata*; A, longitudinal section through the foregut; B, section of tip of proboscis showing sphincters; C, section of portion of the inner wall of the rhynchodeum, showing the differentiation in epithelium from that similar to the proboscis wall, to that typical of the lining of the rhynchocoel. Abbreviations: bm, buccal mass; bts, buccal tube sphincters; con, circum-oral nerve ring; mb, muscular bulb; od, odontophore; oe, oesophagus; p, proboscis; rhs, rhynchostomal sphincter; rs, radular sac; sg, salivary gland; tec, tall epithelial cells; vg, venom gland.

Sac-like enlargement of buccal tube

One other character associated with the gripping of marginal teeth at the proboscis tip, is the presence of a sac-like enlargement of the anterior or middle parts of the buccal tube. It is found in different 'lower' turrids (Kantor & Taylor, 1991) as well as *Mangelia nebula* (Sheridan *et al.*, 1973) and Conidae (*Conus catus* (Greene & Kohn, 1989) and *C. ventricosus*). Usually, the epithelium lining the enlargement is formed of much taller cells than in the rest of the buccal tube. These cells tightly surround the single radular teeth whilst they are being held at the proboscis tip and may afford a better grip. In *Splendrillia chathamensis*, Sysoev & Kantor (1989) found the base of tooth adhering to a pad of epithelial cells.

Protrusive lips of proboscis/ buccal tube

In a few species, the inner lining of the outer lips of the proboscis can be protruded. For example, in *Turricula nelliae spurius*, the lips (Fig. 11) are densely covered by paddle or discocilia, which according to Haszprunar (1985) may indicate the presence of chemosensory cells. Similar protrusive lips are also found in *Lophiotoma leucotropis* and probably in *Aforia aulaca alaskana* (Sysoev & Kantor, 1987).

In relaxed specimens of *Mangelia powisiana*, a sac consisting of a single layer of cells is protruded from the proboscis

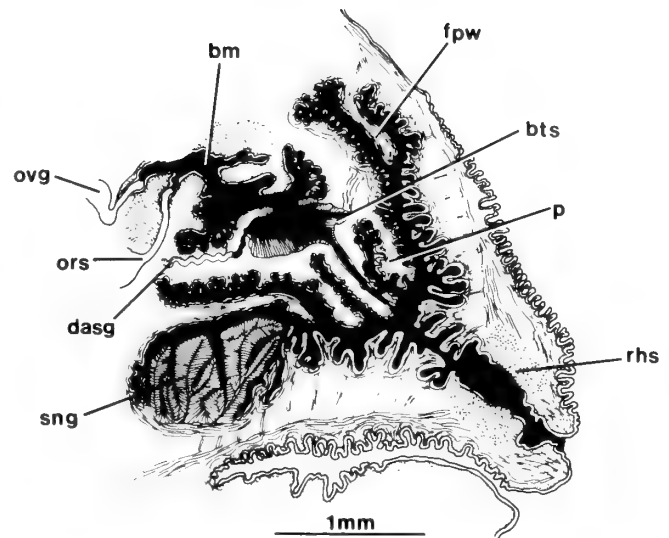


Fig. 7 *Conus ventricosus*; longitudinal section of the foregut showing the proboscis retracted into the rhynchodeum. Abbreviations: bm, buccal mass; bts, buccal tube sphincter; dasg, duct of accessory salivary gland; fpw, fold of proboscis wall; ors, opening of radular sac; ovg, opening of venom gland; p, proboscis; rhs, rhynchostomal sphincter; sng, snout gland.

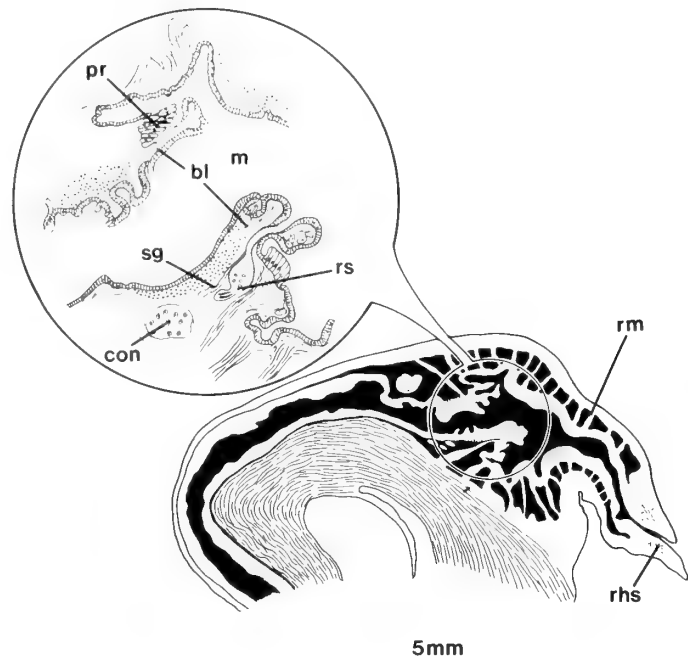


Fig. 8 *Gymnobela emertoni*; longitudinal section of the foregut showing the remnants of the proboscis, buccal lips and vestigial radular sac. Abbreviations: bl, buccal lips; con, circum-oral nerve ring; m, mouth; pr, reduced proboscis; rhs, rhynchostomal sphincter; rm, radial muscles in rhynchodeal wall; rs, radular sac; sg, salivary gland.

tip (Fig. 12). This sac is covered in granule-like structures which are formed from single cells with large rounded nuclei. The distinctive epithelial cells seen at the proboscis tip of *Mangelia nebula* by Sheridan *et al.* (1973) may be the same structure but in a more contracted position. The function of this sac structure is not known.

Position of the buccal mass

Three conditions are known in the Conoidea;

a) Buccal mass situated at the base of the proboscis (Fig. 1)

For three reasons we consider this condition to be the primitive state within the Conoidea. Firstly, a basal buccal mass is found in species of the subfamily Drilliinae, which with five teeth in each radula row, are considered to possess the least-derived type of radula. Secondly, and also in the Drilliinae, there is a muscular connection between the retractor muscle of the radular sac and the columellar muscle (Kantor, 1990). This is a condition found in some meso- and archaeogastropods, as for example in *Littorina*, *Cryptonatica* and *Tegula* (Fretter & Graham, 1963; Kantor, unpublished observations). In most other probosciform gastropods, including those turrids where the buccal mass lies within the proboscis, this connection is broken and the radula is connected by muscles to the walls of the proboscis. Finally, the basal buccal mass is a character-state shared amongst most of the subfamilies of Turridae, along with the Terebridae, Pervicaciidae and Conidae.

b) Buccal mass located within the proboscis

In *Clavatula diadema* (Clavatulinæ), the buccal mass lies within the proboscis, but in a proximal position (Kantor, 1990, fig. 8). In *Clionella sinuata* (Clavatulinæ), *Pilsbryspira nympha* (Zonulispirinae) and *Funa latisinuata* (Crassispirinae), it lies more anteriorly, about half way along the proboscis (Figs 6 & 14). In *Strictispira paxillus* (Strictispiri-

nae) (Fig. 13), *Toxiclionella tumida* (Clavatulinæ) (Kantor, 1990 fig. 4), and *Turricula nelliae spurius* (Cochlespirinae) (Taylor, 1985; Miller, 1990), the buccal mass lies in a distal position near the tip of the proboscis.

The distally shifted position of the buccal mass in these few turrids is a derived condition, being found only in some species of the subfamilies Clavatulinæ, Cochlespirinae Zonulispirinae and Strictispirinae.

c) Buccal mass situated a long way to the posterior of the proboscis base (Kantor, 1990, fig. 1).

This condition is found only in *Hormospira* (Pseudomelatominæ) and described by Kantor (1988).

Elongation of the oesophagus to the anterior of the circum-oral nerve ring

In some turrids the oesophagus is elongated into a curved loop between the base of the proboscis and the circum-oral nerve ring (Fig. 14). This elongation is found in those turrids with a buccal mass situated within the proboscis, and allows forward movement of the buccal mass on protraction of the proboscis. This condition is found in Clavatulinæ, Strictispirinae, *Turricula nelliae spurius* (Cochlespirinae), Crassispirinae such as *Funa latisinuata*, and *Pilsbryspira* (Zonulispirinae).

Buccal lips (inner buccal tube)

These consist of muscular extensions of the anterior walls of the buccal mass, which protrude as a tube into the lumen of the buccal tube (Figs 1 & 9). In *Oenopota levidensis* where the buccal lips are long (Shimek, 1975), they form a second 'proboscis' within the true proboscis. At full contraction of the true proboscis, the tube formed by the buccal lips protrudes through the mouth. Shimek (1975) called this secondary 'proboscis' the buccal tube. Various developments

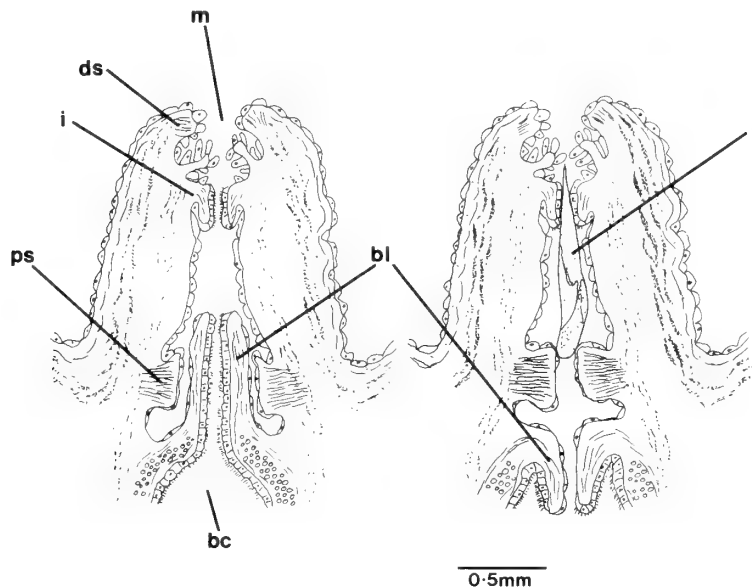


Fig. 9 *Mangelia nebula*; longitudinal section through the proboscis. A, with buccal lips protracted; B, radular tooth in proboscis and buccal lips withdrawn into the buccal cavity. After Sheridan *et al.* (1973, fig. 7) & Delaunoy & Sheridan (1989, plate II). Abbreviations: bc, buccal cavity; bl, buccal lips; ds, distal sphincter of buccal tube; i, buccal tube introvert; m, mouth; ps, posterior sphincter of buccal tube; t, radular tooth.

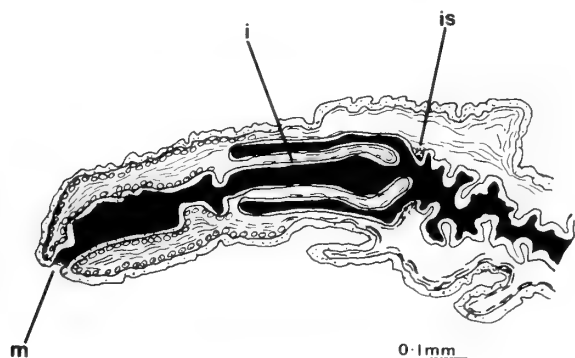


Fig. 10 *Eucithara stromboides*; longitudinal section through the anterior end of the proboscis showing the buccal tube introvert. Abbreviations: i, introvert; is, intermediate sphincter; m, mouth.



Fig. 11 *Turricula nelli spurius*; extended proboscis, showing the inner ring of the protrusive lips. Scale bar = 100 μ m.

of the buccal lips from a short tube to long proboscis-like structures, are seen in species of the subfamily Mangeliinae. Sections of *Mangelia nebula* (Sheridan *et al.*, 1973; Delaunois & Sheridan, 1989) show that the buccal lips can be inverted into the buccal cavity (Fig. 9b). In the genus *Aforia* (Cochlespirinae), some species have well developed buccal lips, but in others they are absent (Sysoev & Kantor, 1987).

In some conoideans lacking a proboscis and radula (e.g. *Terebra gouldi* (Miller, 1975)), the buccal lips are enlarged and consist only of circular muscles. They have the appearance of, and may be confused with, the true proboscis.

The buccal cavity and radular apparatus

From the true mouth, the buccal tube leads to a well-defined chamber, the buccal cavity, which is surrounded by thick walls of circular muscle. The radular diverticulum usually opens ventrally into the buccal cavity. It consists of the radular sac within which the radular teeth are formed, and in less-derived turrids, an odontophore and sublingual pouch (Fig. 15). The latter is the site where degeneration of the radular teeth and ribbon occurs. The buccal sac is defined (Shimek, 1976), as that part of the radular diverticulum that lies between the buccal cavity and the entrance of the salivary ducts.

In higher turrids without a radular membrane and odontophore, the sublingual pouch is transformed into a caecum for the storage of radular teeth prior to their use at the proboscis tip.

Radula caecum (often called short arm of the radula sac)

This is a diverticulum which branches off the anterior end of the radular sac, in which detached radular teeth are stored prior to their use at the proboscis tip (Fig. 15). We regard this structure as a homologue of the sublingual pouch found in other gastropods with a radular ribbon. A radular caecum is present in higher turrids, for example the subfamilies Mangeliidae, Daphnellinae, and Borsoniinae and also in Conidae and some Terebridae.

Shimek (1976) showed that the caecum in *Oenopota levinsensis* is divided longitudinally by a septum. We have seen this structure only in *Micantapex parengonius* (Borsoniinae).

Radular membrane

In general, the 'lower' turrids have a robust radular membrane, whilst in 'higher' turrids, it is thin or absent. However, even in 'lower' turrids, the strength of the membrane varies considerably between taxa and we recognise only the presence or absence of the membrane as a functionally important character.

A radular membrane is absent in the subfamilies Borsoniinae, Mangeliinae, Daphnellinae, Conorbinae, Clathurellinae, Taramiinae, Conidae and most Terebridae.

Odontophore

An odontophore with cartilages is present in many lower turrids (Drilliinae, Pseudomelatominae, Strictispirinae, Clavatulinae, Turrinae, Cochlespirinae, Crassispirinae), the Pervicaciidae, and a few species of *Hastula* (Terebridae), but is absent in higher turrids, Conidae and most other Terebridae.

If an odontophore is present, then the cartilages may be either fused, or separated at the anterior end. If the cartilages are separated, they are joined by a muscular connection. We have seen fused odontophoral cartilages in *Lophiotoma*, Pseudomelatominae, *Splendrillia*, *Clavus sp.*, *Inquisitor* and *Funa* spp., *Toxiclionella* and some *Aforia* species. Two separate cartilages are usually present in species of Clavatulinae (except *Toxiclionella*), *Strictispira paxillus* (Strictispirinae) (Fig. 13). In *Aforia lepta* (Cochlespirinae), only the muscle is present, over which the radular membrane bends (Sysoev & Kantor, 1988).

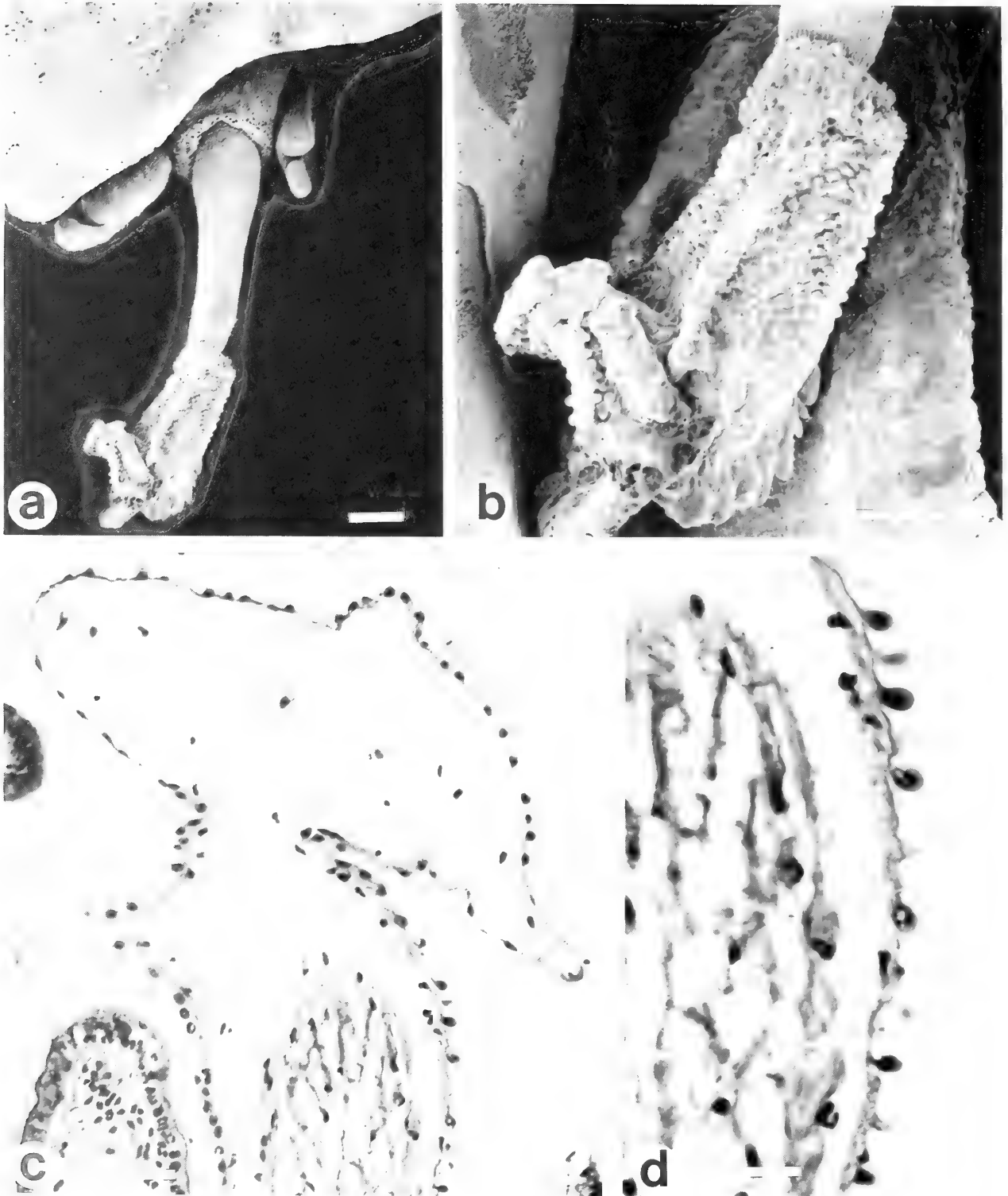


Fig. 12 *Mangelia powisiana*; a, relaxed specimen showing sac-like structure at distal end of extended proboscis. Scale bar = 100 μm . b, detail of sac body with warty external surface. Scale bar = 100 μm . c, section of the sac showing the thin epithelium with granule structures produced by single cells with large nuclei. Scale bar = 50 μm . d, detail of c. Scale bar = 10 μm .

Radula

The radula has been by far the most studied of the organs of the foregut and there are many published illustrations of conoidean radular teeth (e.g. Powell, 1966; McLean, 1971; James, 1980; Bandel, 1984; Bogdanov, 1990; Nybakken, 1990 and Taylor, 1990). Shimek & Kohn (1981) classified turrid radulae into a number of functional groups and attempted a cladistic analysis of radular characters. However, amongst the 'lower' turrids there is little evidence from direct observations to support their functional categories. Indeed, recent evidence shows that even in the least-derived radulae which possess a strong radular ribbon, the marginal teeth can be held singly at the proboscis tip in a stabbing position (Kantor & Taylor, 1991).

A radula is present in most Turridae, all Conidae, possibly all Pervaciidae and some Terebridae. It is absent in some species of Daphnellinae, Taraninae and many species of Terebridae (Miller, 1970; Taylor, 1990). The phenomenon of radula-loss in conoideans has recently been reviewed by Kantor & Sysoev (1989).

For the purposes of the present analysis, we have attempted to recognise different morphological types of radula, without any functional interpretation.

The radula of the Drilliinae, which is usually regarded as the least-derived condition within the Turridae, has five teeth in each transverse row (Fig. 16a). These teeth are usually referred to as central, lateral and marginal teeth respectively; although there are different interpretations (Kantor, 1990; Starobogatov, 1990). We consider the morphology of each of these teeth in turn.

1. Central tooth

A central tooth is present in species of Drilliinae, Pseudomelatominae, Turrinae, Clavatulinae, and Cochlespirinae. It can

be reduced and lost in some species of these subfamilies except Pseudomelatominae. (i) In the Pseudomelatominae, the central tooth is fairly robust and broad, with a large curved central cusp and sometimes smaller cusps at either edge (Fig. 17e & f). (ii) In the Drilliinae the central tooth is robust, but small and narrow (Fig. 16b & d), usually with a prominent central cusp and a number of subsidiary cusps. (iii) In the Turrinae and Clavatulinae (Figs 18a–d, 19a & b), the central tooth appears broad, but apart from a spine-like central cusp is poorly defined. The central cusp appears homologous with the central tooth of the Drilliinae, but the insubstantial, lateral 'wings' may represent vestiges of lateral teeth which have fused with the central tooth. Alternatively, the whole tooth might be homologous with the central tooth of the Pseudomelatominae, the central cusp remaining prominent, but the lateral edges becoming less substantial. Study of the ontogeny of the radula in these taxa might distinguish between these alternative possibilities.

2. Lateral teeth

We recognise two types of lateral teeth. (i) In what is considered to be the least-derived condition, most species of Drilliinae have large, multicuspitate, comb-like, lateral teeth (Fig. 16a,c,e). However, reduced teeth are found in some drilliine species (Bandel, 1984, fig. 306). (ii) In *Antiplanes* (Cochlespirinae), the radula folds along the middle of the radular ribbon, suggesting that the poorly defined, plate-like teeth are in fact laterals (Kantor, 1990; Kantor & Sysoev, 1991, figs 26–27, 30–32). These 'teeth' were not visible on S.E.M. preparations. Similar, poorly defined, lateral 'teeth' are also present in optical preparations of *Crassispira* and *Crassiclava* of the Crassispirinae (Maes, 1983 fig. 31 & 37, p. 322; Kilburn, 1988, p. 239).

In all other subfamilies of Turridae, Pervaciidae, Terebridae and Conidae, lateral teeth are absent.

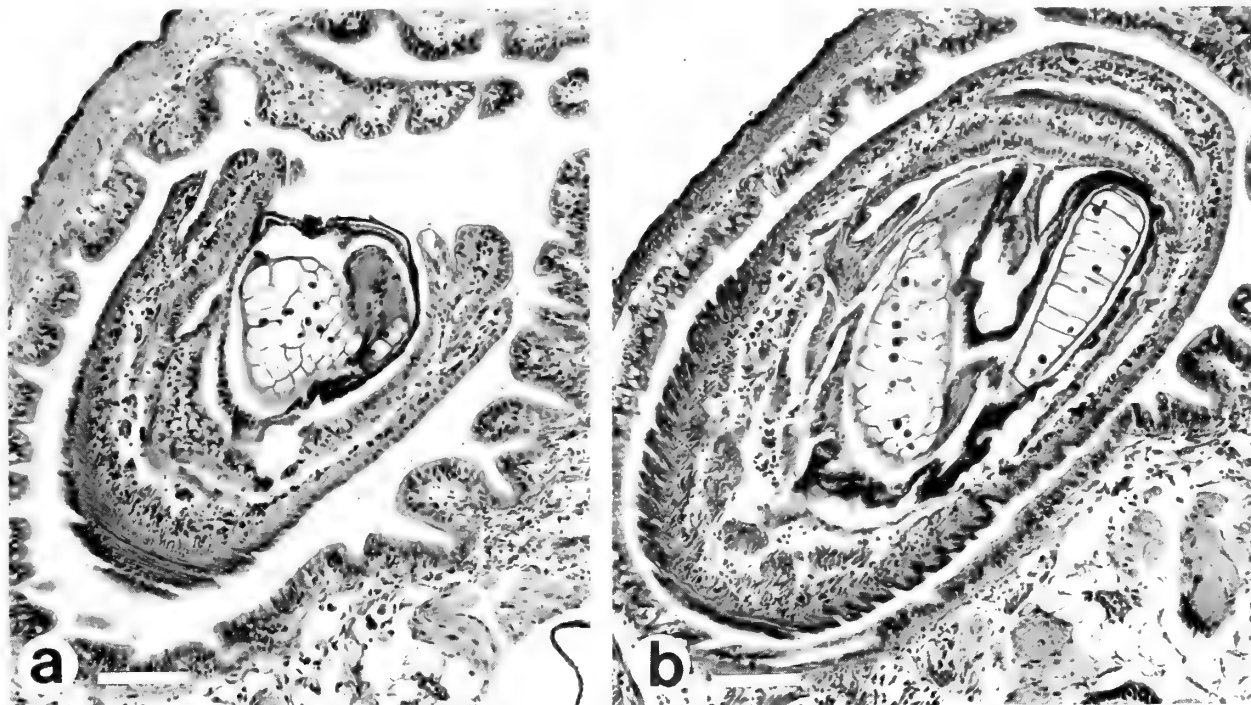


Fig. 13 *Strictispira pauxillus*; transverse section of the rhynchoel and the proboscis tip. a, mouth with distally-situated radula and virtually no bucal tube. Scale bar = 100 μ m. b, section of the proboscis slightly to the posterior of (a) showing the two large odontophoral cartilages. Scale bar = 100 μ m.

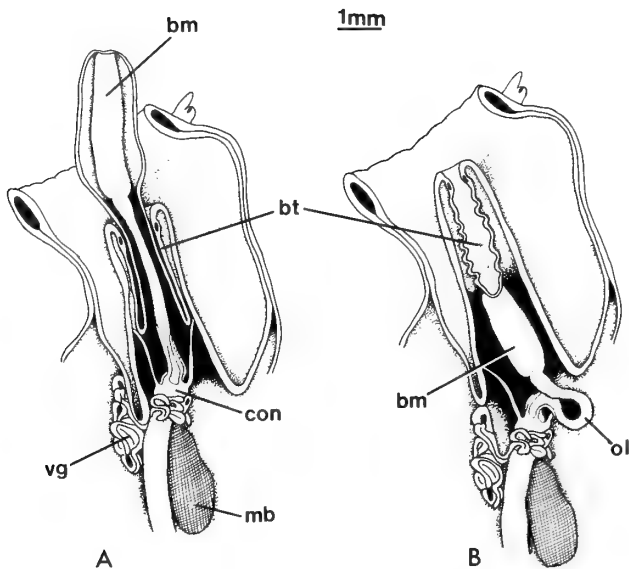


Fig. 14 *Funa latisinuata*; anterior alimentary system. A, proboscis with buccal mass in extended position; B, with buccal mass in retracted position and showing the loop of the oesophagus situated to the anterior of the nerve ring. Modified from an unpublished drawing by J. Miller. Abbreviations: bm, buccal mass; bt, buccal tube; con, circum-oral nerve ring; mb, muscular bulb; ol, oesophageal loop; vg, venom gland.

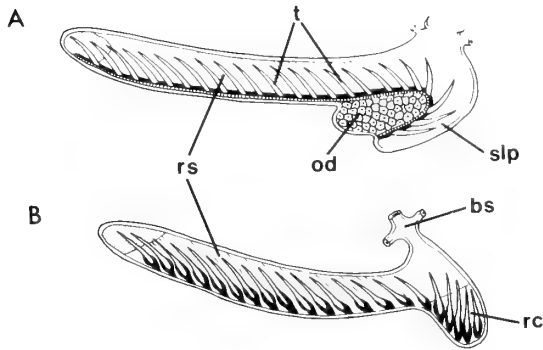


Fig. 15 Diagrammatic section through the radular sac. A, in turrids possessing an odontophore; B, turrids lacking an odontophore, but with a radula caecum. Abbreviations: bs, buccal sac; od, odontophore; rs, radular sac; rc, radula caecum; slp, sublingual pouch; t, radular teeth. Buccal sac is that portion of the radular sac lying between the entrance of the salivary ducts and the buccal cavity.

Fig. 16 Radulae of Drilliinae. a, half radula row of *Clavus* sp. from Guam showing blade-like marginal teeth, comb-like lateral teeth and the small central tooth. Scale bar = 50 μ m. b, central tooth of *Clavus unizonalis*. Scale bar = 5 μ m. c, central and part of lateral teeth of *Spirotropis monterosatoi*. Scale bar = 20 μ m. d, central tooth of *S. monterosatoi*. Scale bar = 10 μ m. e, single lateral tooth of *S. monterosatoi*. Scale bar = 20 μ m. f, marginal teeth of *S. monterosatoi*. Scale bar = 20 μ m.

Fig. 17 Radulae of Strictispirinae and Pseudomelatominae. a, radula of *Strictispira paxillus*. Scale bar = 50 μ m. b, marginal teeth of *Strictispira stillmani*. Scale bar = 50 μ m. c, radula of *Cleospira ochsneri*. Scale bar = 50 μ m. d, marginal teeth of *Strictispira paxillus* seen from side. Scale bar = 50 μ m. e, radula of *Pseudomelatoma penicillata*. Scale bar = 100 μ m. f, central tooth of *P. penicillata* seen from side. Scale bar = 10 μ m. (see p. 138)

3. Marginal teeth

In most conoideans the marginal teeth are the principal functional teeth. Although diverse in appearance, they can be divided into three broad categories of solid, wishbone and hollow. There may be several subdivisions of each category. Teeth of the first category are represented by a single, flat, distally acute plate. Wishbone teeth are characterised by two plates connected to each other. Hollow teeth are distinguished by a cavity within the tooth.

a) Solid marginal teeth

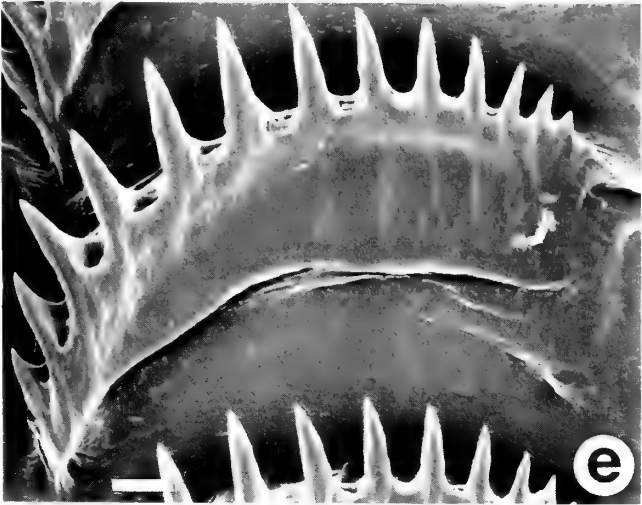
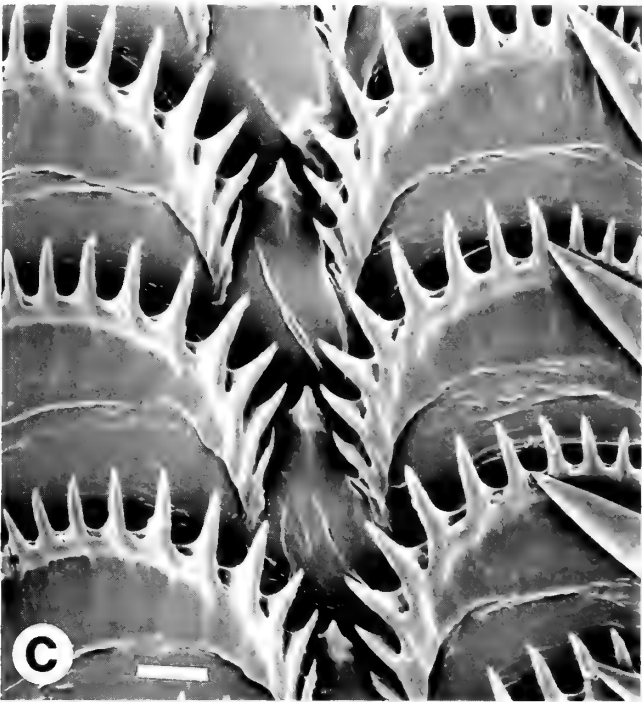
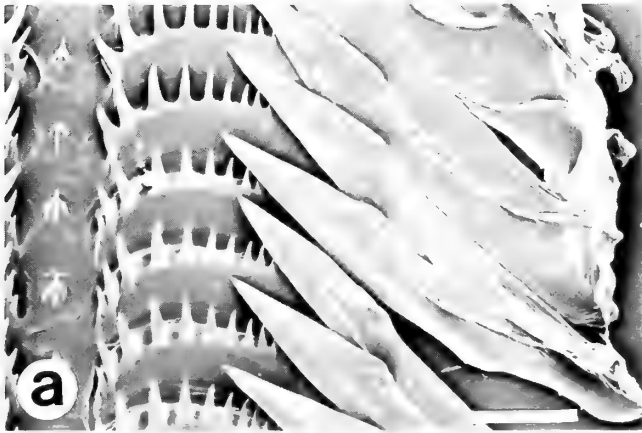
We recognise four main categories of solid teeth. (i) Simple, flat teeth, often with a simple, blunt barb (Figs 16a, f, Fig. 20a). This type of tooth is common in the Drilliinae. (ii) Simple teeth as in (i), but with the lateral edges of the tooth curved to form a channel or gutter. This type of tooth has been recorded from *Drillia cydia* (Powell, 1966, fig 81; Maes, 1983, fig. 28). (iii) Simple, solid teeth, which are curved and pointed (Fig. 17e). This type of tooth is found only in Pseudomelatominae (Kantor, 1988) and the Pervaciidae (Taylor, 1990). (iv) Simple, awl-shaped teeth with a large base and pointed tip and a spatulate process midway along the tooth (Figs 17a–d). This type of tooth has been found only in the subfamily Strictispirinae.

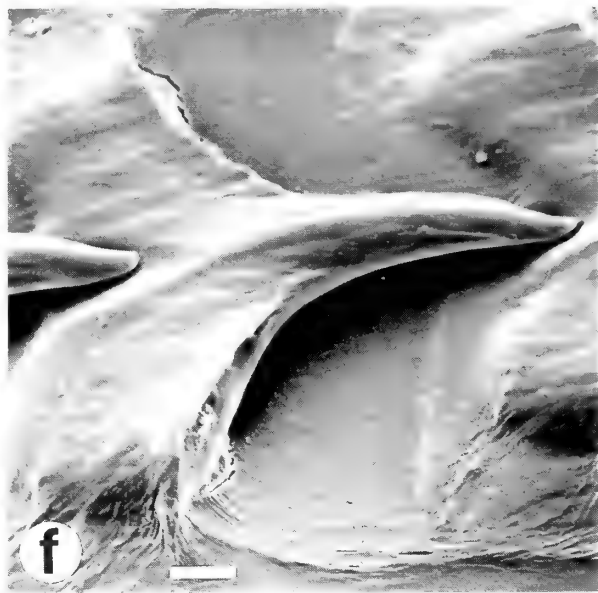
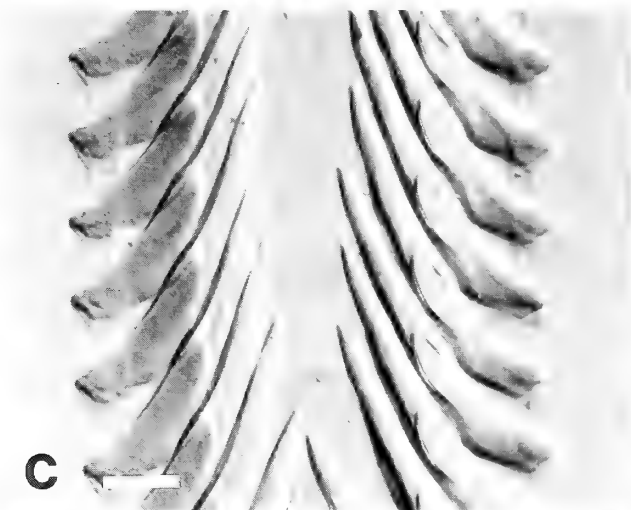
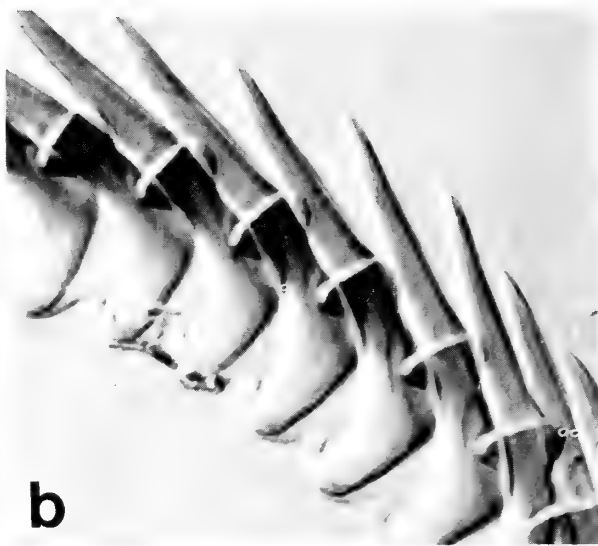
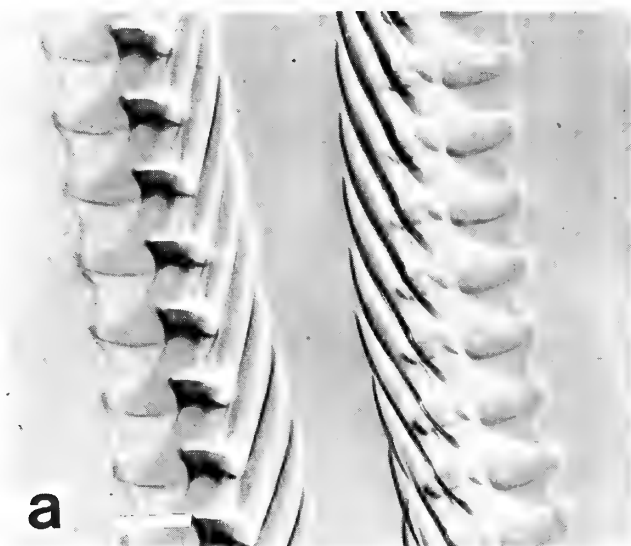
b) Wishbone teeth (sometimes called duplex teeth)

In this type of dentition, the marginal teeth consist of two parts, comprising the main tooth together with an accessory limb. Published illustrations suggest a great variety of form in wishbone teeth, but S.E.M. observations show that some of this variety results from artifacts produced by the transparency of light microscopy and by different positions of teeth (often with displaced tooth parts) in preparations.

We recognise four basic types of wishbone teeth:

(i) Broad, slightly curved teeth, sometimes with a blunt barb (Fig. 20 b–d). The lateral edges of the teeth are thickened, with a thin accessory limb attached to the main tooth at the anterior and posterior ends. This type of tooth is common in some Crassispirinae such as *Inquisitor*, *Paradrillia* and *Funa*, where the size and shape of the accessory limb varies considerably between species (Kilburn, 1988). Because the main limb is similar to the marginal teeth of the Drilliinae, we suggest this as the least-derived type of wishbone tooth. (ii) The teeth of this type are robust, short and curved, sometimes with a knife-like cutting edge on the main limb and a large accessory limb (Figs 18a,c; 19a,d). Teeth of this type are found in species of Turrinae, Clavatulinae, and Cochlespirinae. (iii) Teeth that may be modified wishbone teeth have been illustrated for *Ptychobela nodulosa* and *P. suturalis* by Kilburn (1989, figs 17–19). The teeth are awl-shaped without barbs, with apparently two nearly equi-size limbs joined to form a central channel. An S.E.M. study of these teeth is needed to clarify their morphology. (iv) In the radula of *Ptychobela griffithi* the teeth appear to be robust and solid with a simple barb (Fig. 22a), but they may in fact





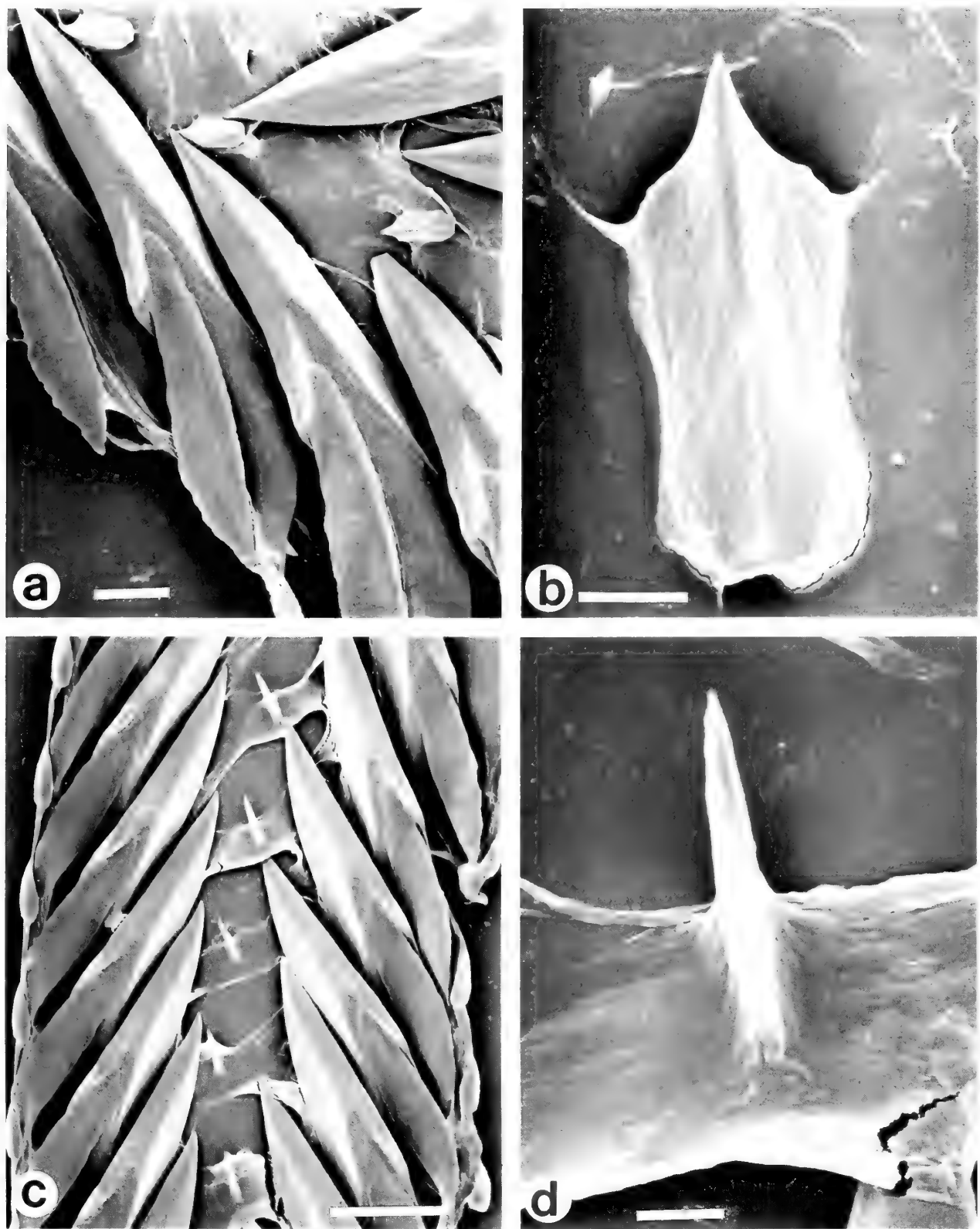


Fig. 18 Radulae of Clavatulinae and Cochlesprinae. a. *Clionella sinuata*; wishbone marginal and small central teeth. Scale bar = 50 μ m. b. *Clionella sinuata* small central tooth. Scale bar = 10 μ m. c. *Turricula nelli spurius*, radula with wishbone marginal teeth and central tooth with spine-like cusp and lateral flanges. Scale bar = 50 μ m. d. *T. nelli spurius* central tooth. Scale bar = 5 μ m.

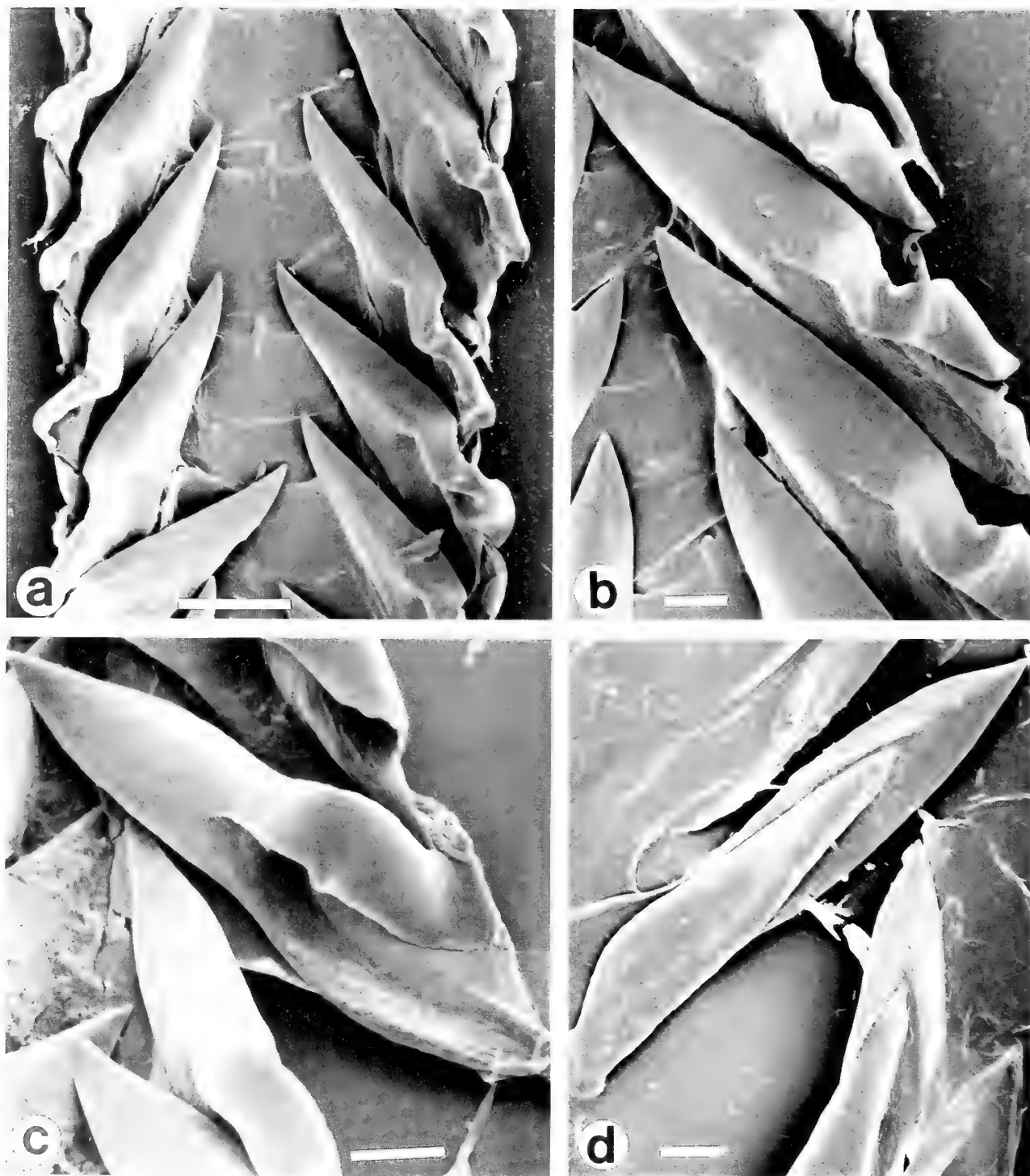


Fig. 19 Wishbone teeth of Turrinae and Cochlespirinae. a. radula of *Gemmula deshayesi*. Scale bar = 50 μm . b. marginal tooth of *Gemmula deshayesi* Scale bar = 20 μm . c. marginal tooth of *Lophiotoma acuta* Scale bar = 10 μm . d. marginal tooth of *Antiplanes sanctioannis*. Scale bar = 20 μm .

be formed from two pieces as in *Ptychobela suturalis* (see above). Lack of material precluded further study of this and the type iii wishbone teeth.

c) Hollow teeth

There is a great diversity of detailed variation in the form of hollow marginal teeth even within a single genus (see for example, James (1980) and Nybakken (1990) for *Conus* and Bogdanov (1990) for *Oenopota*). However, for the purposes of this analysis we recognise only five main types of hollow teeth. (i) Teeth of this type are long, slender, and enrolled,

with a small base. The base is not differentiated morphologically and is not solid. The distal end of the tooth may be simple, or more or less, elaborately barbed (Figs 22e,g). There is an opening near the distal tip and a second opening placed more or less terminally at the proximal end. The shaft of *Hastula hectica* is perforated by holes (Taylor, 1990, fig. 2). For some *Conus* species, Nybakken (1990) has shown that during ontogeny, the hollow, rolled teeth develop from open, guttered forms and become progressively more elaborately barbed. Hollow teeth of Type i are found in species of

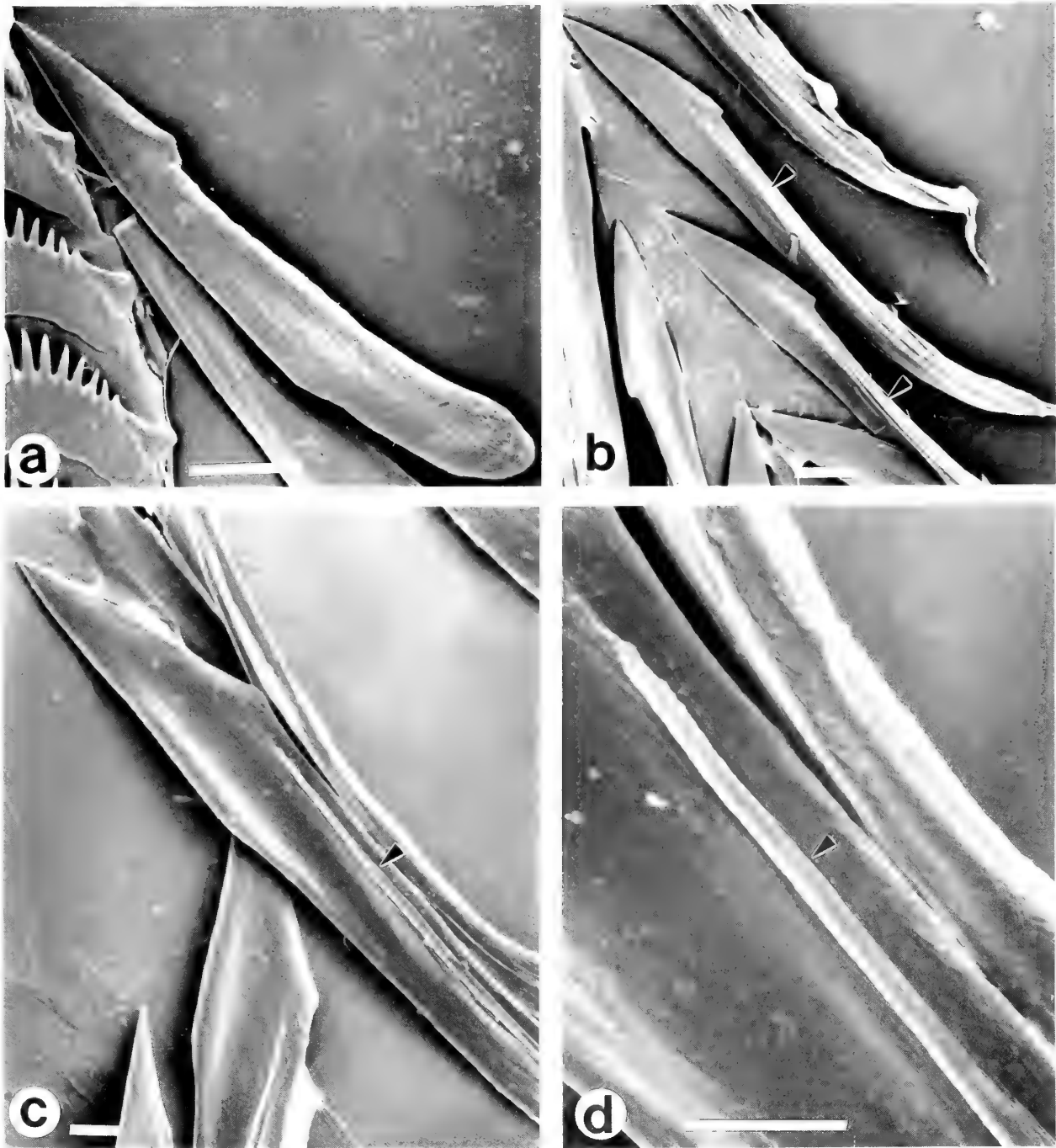


Fig. 20. Radulae of Clavinae and Crassispirinae. a. marginal tooth of *Drillia rosacea*. Scale bar = 50 µm. b. *Funa latisinuata*; blade-like marginal teeth with thin accessory limb. Scale bar = 50 µm. c. *Vexitomina garrardi*; part of blade-like marginal tooth with accessory limb (arrowed). Scale bar = 10 µm. d. enlargement of (d) showing accessory limb. Scale bar = 10 µm.

Borsoniinae, Clathurellinae, *Toxiclionella* (Clavatulinae), Conidae, and Terebridae (ii) Hollow teeth of this second type are often short with a large, solid base (Fig. 23). The tooth cavity opens laterally between the shaft and the base. There are frequently side projections around the base (hilted dagger form of Powell 1966), often with a large irregular solid 'root' projecting from the base (Fig. 23e,f). These teeth are often only partially enrolled. Barbs may be present. Marincovich (1973) records rows of holes in the teeth of *Agathotoma ordinaria* (Mangeliinae). Teeth of Type ii are found in the subfamilies Mangeliinae, Oenopotinae (Bogdanov, 1990, figs 407–438), Thatcheriinae, and the radulate Daphnellinae. (iii) Teeth of this type are partially enrolled at the base, but solid and blade-like in the distal part (Fig. 22b). This type of tooth is presently known only from *Hastula bacillus* (Taylor & Miller, 1990). It may represent a transitional form between the solid teeth found in the Pervicaciidae and the hollow teeth of the Terebridae. (iv) This type of tooth is loosely enrolled to form a central channel, with a simple barb at the tip. The tooth was first described in detail from *Imaclava unimaculata* (Clavinae) by Shimek & Kohn (1981 fig. 7). *Imaclava* otherwise has comb-like lateral teeth as in typical Clavinae. Similar teeth are present in other species of *Imaclava* (McLean, 1971, fig. 7). (v) Enrolled teeth with a complex appearance are seen in *Pilsbryspira nympha* (Zonulispirinae) (Fig. 21). Although these are hollow teeth with a small barb, the shaft is complex and appears to be formed by partial enrolling of two units (Fig. 21b). The tooth may be derived by the enrolling of the elongate wishbone teeth typical of the Crassispirinae. (vi) Vestigial teeth, semi-enrolled, with a gutter along the tooth. Teeth of this type are considered by Bogdanov (1990) as

derived from the distal part of the shaft of Type ii teeth. This type of tooth is found in *Propebela turricula* and *P. harpularia* (Oenopotinae) (Bogdanov, 1990, figs 41, 433).

Glands of the foregut

Salivary glands

Salivary glands are present in most turrids, *Conus* and the radulate species of Terebridae and Pervicaciidae. In most species a pair of glands is present, but these may be fused together. The salivary ducts always open into either side of the buccal sac (Fig. 1). In *Turricula nelliae spurius*, which has a distal buccal mass, the salivary glands are contained within the proboscis and attached to the oesophagus (Miller, 1990).

In most conoideans, the salivary glands are acinous, but in the Mangeliinae, Thatcheriinae, Daphnellinae and *Haedroleura septangularis* (Crassispirinae) the glands consist of long, convoluted, single tubes (Sheridan *et al.*, 1973; own observations).

Turrids without a radula also lack salivary glands, but in the Terebridae, glands are present in some radula-less forms, such as *Terebra gouldi* and *T. maculata* (Miller, 1970, 1975).

Accessory salivary glands

These are known in a few species of Turridae, some Conidae (Marsh, 1971; Schultz, 1983) and Terebridae (Taylor & Miller, 1990; Taylor, 1990). They have a similar histology to the accessory salivary glands found in other neogastropod families such as the Muricidae (Andrews, 1991). Further-

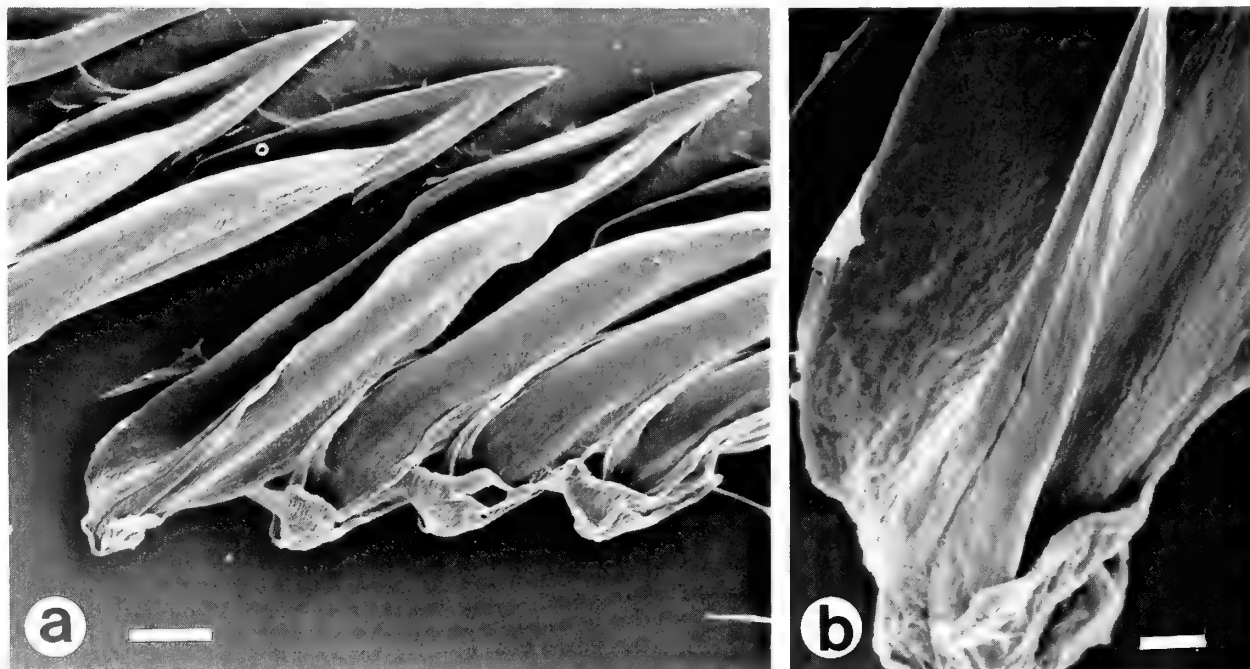
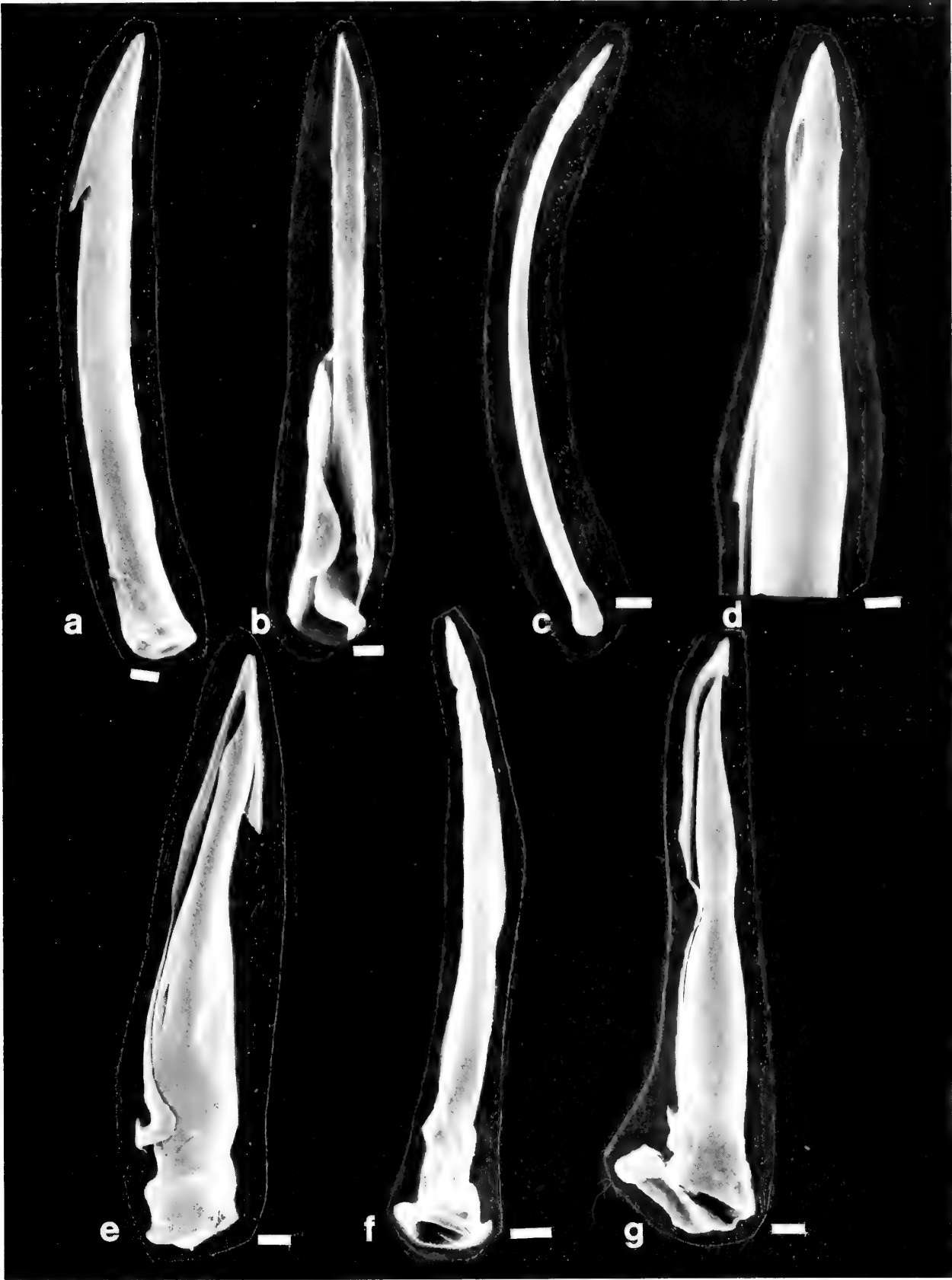
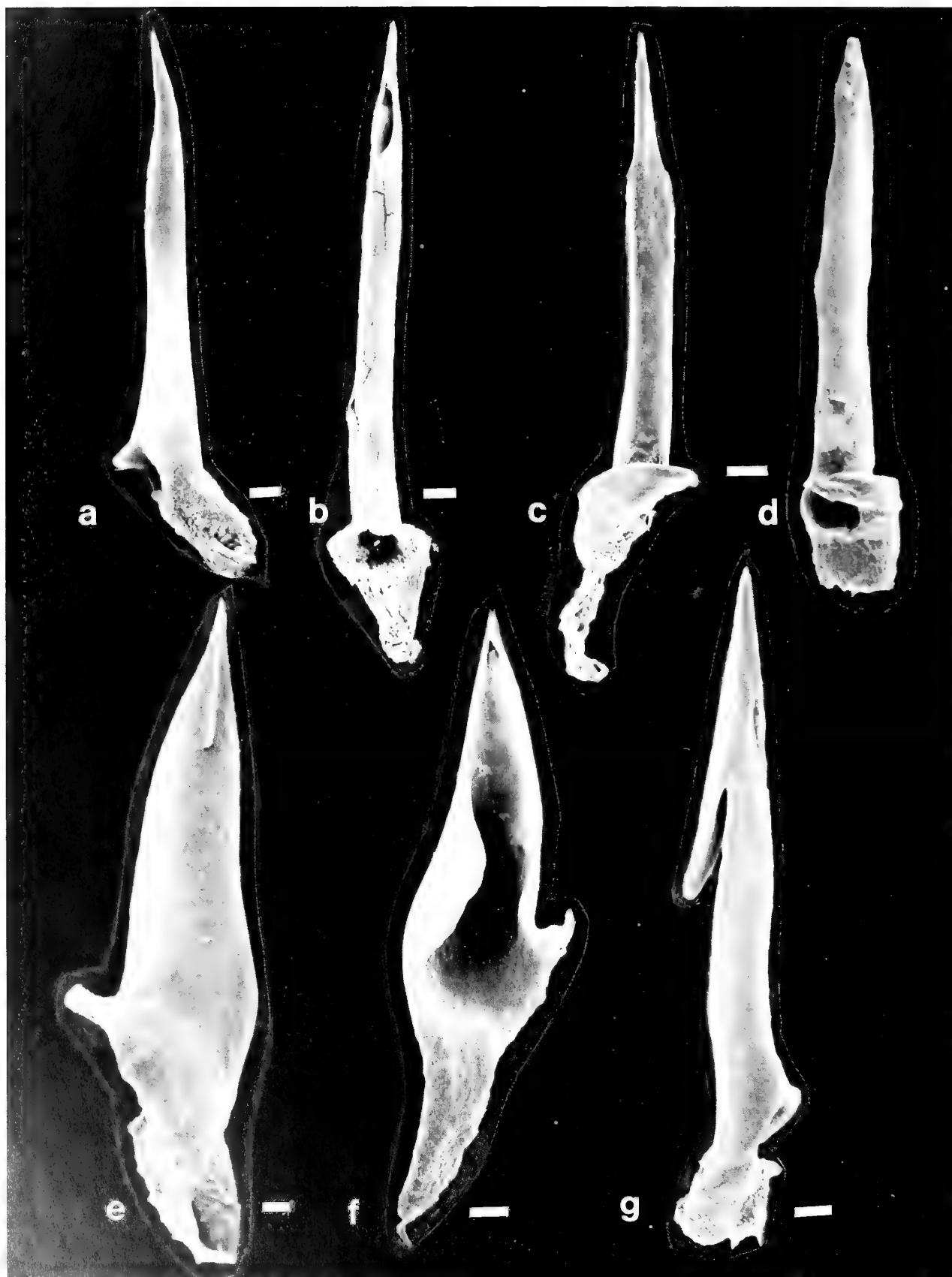


Fig. 21. Enrolled teeth of *Pilsbryspira nympha*. a. several adjacent marginal teeth. Scale bar = 25 µm. b. detail of base of tooth showing double structure (arrow) suggesting that tooth may be formed by the enrolling of wishbone teeth. Scale bar = 5 µm.

Fig. 22. Single marginal teeth from Turridae and Terebridae. a. *Ptychobela griffithi*. Scale bar = 10 µm. b. *Hastula bacillus*. Scale bar = 5 µm. c. *Glyphostoma candida*. Scale bar = 50 µm. d. enlargement of the tip of the *G. candida* tooth. Scale bar = 10 µm. e. *Genota mitraeformis*. Scale bar = 20 µm. f. *Terebra babylonica*. Scale bar = 20 µm. g. *Conus ventricosus*. Scale bar = 20 µm.





more, the ducts from the accessory glands open near the tip of the buccal tube, which is the homologous position to that found in other neogastropods.

Within the Turridae, we have observed accessory salivary glands in only two subfamilies: the Borsoniinae (*Scrinium neozelanicum*, *Borsonia ochracea*, and *Micantapex parengoni*) and Cochlespirinae (*Aforia hypomela*, *A. kupriyanovi*, *A. abyssalis*). In the Terebridae, we have seen accessory glands in *Hastula bacillus*, *Terebra babylonia*, *T. funiculata* and *T. subulata* (Taylor, 1990). Usually, only a single gland is found, but two glands are present in *Terebra subulata*.

Venom apparatus (venom gland and muscular bulb)

The long, tubular, and convoluted venom gland is the most conspicuous organ of the conoidean foregut. It always passes through the nerve ring and always opens into the buccal cavity immediately posterior to the opening of the radular sac (Figs 1 & 7). The venom gland is present in most conoideans, except the radulate *Strictispira* (Maes, 1983); *Gymnobela tincta*, which has a vestigial radula; the radula-less turrids from the subfamilies Daphnellinae and Taraninae (Smith 1967; Sheridan *et al.*, 1973; Kantor & Sysoev, 1989), the radula-less Terebridae (Miller 1975; Taylor, 1990) and the radulate Pervicaciidae (Taylor, 1990).

In some species, the histology of the venom gland changes in the anterior portion of its length, after its passage through the nerve ring. The posterior portion is packed with venom granules (Fig. 24), but the anterior portion is duct-like and ciliated (e.g. *Clavatula*, *Clionella*, *Turricula*, *Lophiotoma* and *Pilsbryspira*). This change in histology is usually correlated with the elongation of that part of the oesophagus lying between the nerve ring and buccal mass. In other conoideans, venom granules are present all the way along the length of the gland, sometimes even into the buccal cavity.

Extensive studies have been made of the composition and pharmacology of the venom in a few *Conus* species (review by Oliveira *et al.*, 1990). The composition of the venom is very complex and the results from these studies have a potential utility in phylogenetic analysis. However, no comparable studies yet exist for the Turridae and Terebridae.

Muscular bulb

The muscular bulb (Figs 1 & 6) lies at the posterior end of the venom gland and is present in all those species possessing the gland. Differences between taxa are observed both in the number, orientation and relative thickness of the various muscular layers forming the wall of the bulb. The usual condition is of an outer, circular-muscle layer, a thin, middle connective tissue layer, with an inner longitudinal layer. We have, however, observed other configurations of the muscle layers. For example in *Mangelia* species and *Eucithara*, the outer muscular layer is very thin, but the inner layer very thick. *Daphnella reeveana* has only a single, thin muscle layer, whilst *Conus textile* has four distinct alternating circular and longitudinal muscle layers, three of them lying inside the connective tissue layer.

Additionally, Ponder (1970) mentions that he has observed glandular cells in the epithelium lining the muscular bulb in

Lucerapex (Turridae) and *Maoritomella albula* (Borsoniinae). We have not observed the glandular cells in any turrid we have examined.

Summary of foregut anatomy

From the foregoing discussion, it is clear that there is a great variety of foregut anatomy present within the Conoidea and considerable variation may be present even within species of one subfamily. As a summary, twelve of the main types of foregut configuration are shown diagrammatically in Figs 25 & 26. It should be emphasized that only a relatively small number of conoidean species have been investigated anatomically and it is likely that further types of foregut remain undiscovered. Nevertheless, there are several anatomical characters which define the Conoidea and are present in most representatives (and in all the least derived groups). These are:-

1. The presence of a venom gland.
2. The buccal mass located at the base of the proboscis.
3. The proboscis formed by the elongation of the buccal tube.
4. The presence of a permanent rhynchodeum.
5. The tendency for the loss of central and lateral teeth from the primary five toothed radular row.

FUNCTIONAL MORPHOLOGY OF THE DIGESTIVE SYSTEM AND FEEDING MECHANISMS IN TOXOGLOSSA

As has been outlined in the previous section, the morphology of the digestive system of Conoidea and especially that of the Turridae, is highly varied. These variations in morphology probably reflect differences in feeding behaviour and diet. Apart from *Conus*, conoidean diets are still very poorly known. Indeed, for in excess of 4000 living species of Turridae, feeding information is available for less than 30 species (reviewed by Miller, 1989). These data, derived mainly from gut content analysis, show that turrids feed mainly on errant and sedentary polychaetes and more rarely on other phyla such as sipunculans, nemerteans, and molluscs. Very few direct observations of the feeding process in the Turridae have been made (Pearce, 1966; Shimek, 1883a, b, c; Shimek & Kohn 1980; Miller, 1990). Because of this lack of information, our conclusions concerning the feeding mechanisms of Turridae are based upon analysis of the morphology of the digestive tract and by comparison with species whose feeding mechanism is known.

Our classifications of feeding mechanisms is based upon the following characters listed in order of priority: the presence/absence of venom apparatus (used for immobilizing or killing the prey); the mode of radula function (which may be used solely as a whole organ, as a whole organ with simultaneous use of separate teeth, or as separate teeth only at the proboscis tip); position of the buccal mass (either basal or shifted anteriorly towards the proboscis tip). We recognize

Fig. 23 Hypodermic-type marginal teeth with a large solid bases. a. *Paramontana* sp. Scale bar = 2 μ m. b. *Propebela rugulata*. Scale bar = 10 μ m. c. & d. *Thatcheria mirabilis* Scale bars = 20 μ m. e. & f. *Mangelia powisiana*. Scale bars = 5 μ m G. *Eucithara stromboides*. Scale bar = 10 μ m.

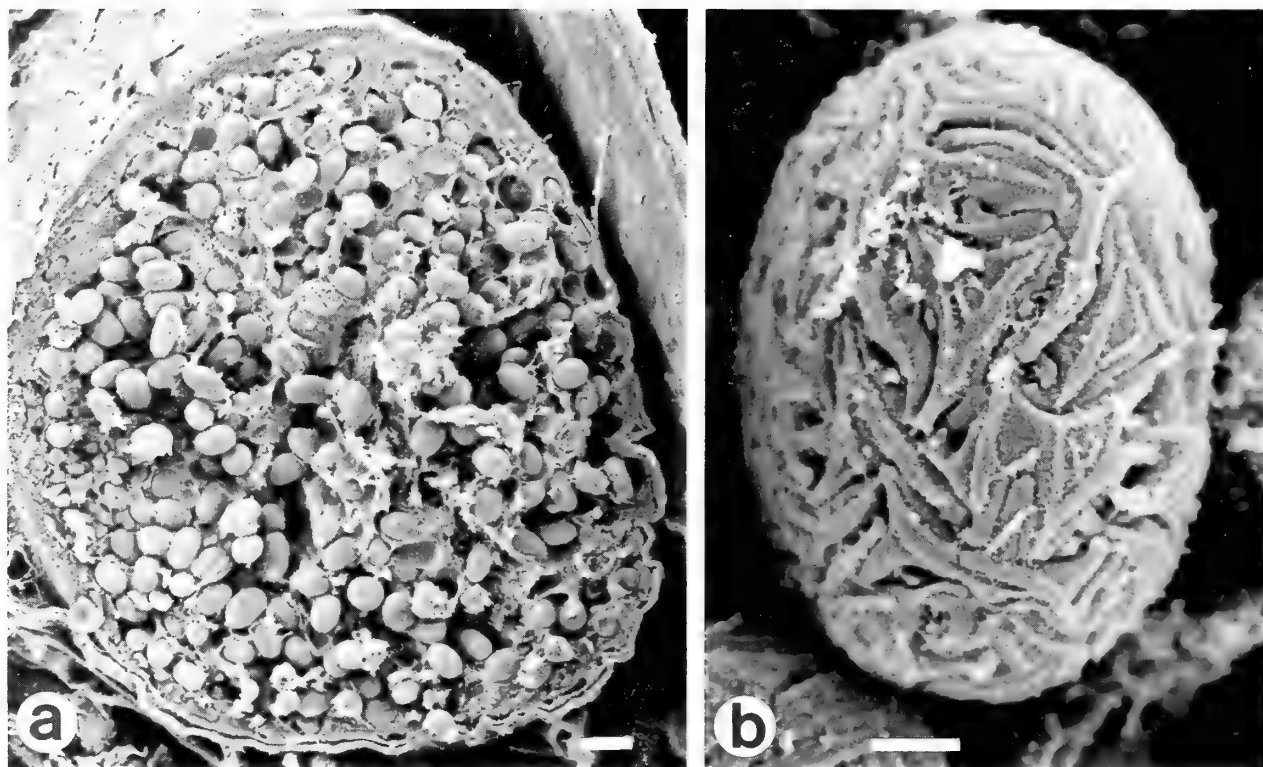


Fig. 24 Venom gland of *Clavus* sp. Guam. a. section through critical-point dried venom gland showing venom granules. Scale bar = 10 μ m. b. enlargement of single venom granule. Scale bar = 1 μ m.

five main and several sub-types of feeding mechanism. Some of these have already been described (Kantor & Sysoev, 1990; Kantor, 1990), but are here partially revised and corrected.

I. Venom gland present

Feeding mechanism Type 1

The first functional type of digestive system and feeding mechanism, that in which the radula is used only as a whole organ in conjunction with the venom apparatus is found among species of Pseudomelatominae and in *Toxiclionella tumida* (Clavatulinae) and can be subdivided into two sub-types.

The first sub-type is characteristic of the Pseudomelatomi-nae, an endemic subfamily from western central America, which includes 3 genera and several species (McLean in Keen, 1971). The anatomy of two species *Pseudomelatoma penicillata* and *Hormospira maculosa* indicates the isolated position of the group among Conoidea (Kantor, 1988). This is particularly clear, from the radular morphology, which consists of a large and well developed central tooth, flanked by large, scythe-like, but solid, marginal teeth.

The buccal mass is situated either at the proboscis base and far ahead the nerve ring in *Pseudomelatoma penicillata*, or in front of the nerve ring and distant from the proboscis base in *Hormospira maculosa*. The anterior part of the digestive tract forms a long curve, either by the elongation of that part of the oesophagus between the nerve ring and the buccal mass (*P. penicillata*), or by the elongation of the posterior part of the buccal tube (*H. maculosa*).

Both species have a well-developed venom gland and although the diet of Pseudomelatominae is unknown, the presence of the large venom gland indicates the predatory mode of feeding. The gastropods also have a muscular proboscis with a wide oral opening but without a sphincter. The absence of the oral sphincter, which is usually used for holding single radular teeth at the proboscis tip (Kantor & Taylor, 1990), coupled with the curved form of the marginal teeth, indicate that the gastropods do not use separate teeth for stabbing the prey. Kantor (1988) supposed that prey capture occurs with the aid of the proboscis tip and is facilitated by the wide and highly extensible oral opening. If this is so, then envenomation of the prey should occur within the anterior part of the proboscis. This facilitates the transport of prey into the buccal cavity, by the peristaltic movements of well-developed circular muscles of the buccal tube.

However, the presence of the elongated part of the oesophagus between the buccal mass and nerve ring in *P. penicillata* may indicate another mode of prey capture. In some turrids (e.g. *Funa latisinuata*, Fig. 14), the presence of such an elongation of the oesophagus is connected with the ability to evert the buccal mass, with the radula, through the proboscis and mouth. It is possible, that *P. penicillata* can evert the buccal mass through the mouth and use the radula directly in prey capture. Envenomation would in this case occur through the damage to the prey made by the radular teeth. Also the very large odontophore (the largest of all the turrids studied) suggests that the radula may also tear the prey.

The morphology of *Hormospira* differs from that of *Pseudomelatoma*, in that the curve is formed by the posterior part of the buccal tube and elongated buccal mass. The

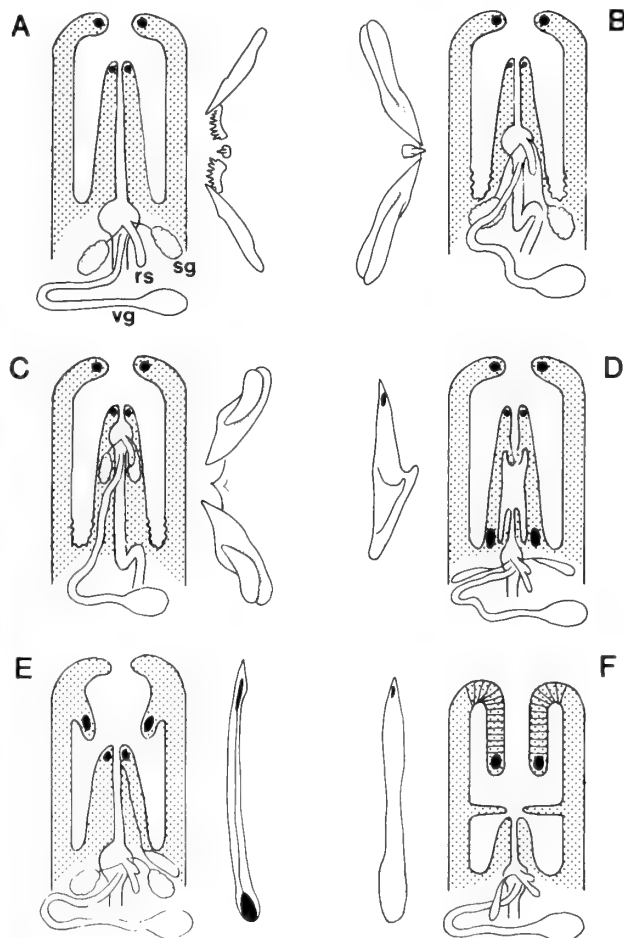


Fig. 25 Diagram (with Fig. 26) summarizing some of the major types of foregut morphology found amongst the Conoidea, with radulae, where present, illustrated alongside. Not to scale. A. *Clavus unizonalis*; B. *Clionella sinuata*; C. *Turricula nelliie spurius*; D. *Mangelia nebula*; E. *Ophiodermella inermis*; F. *Daphnella reeveana*. Abbreviations: asg, accessory salivary glands; sg, salivary glands; rs, radular sac; vg, venom gland; black dots are sphincters.

radular sac is located far behind the base of the proboscis. Therefore, it is doubtful that the buccal mass can be everted through the mouth opening. This species probably catches prey using the proboscis tip. Envenomation could occur either by the squirting of venom through the mouth, when the proboscis is in contact with the prey, or in the anterior part of the proboscis, when the prey is partly swallowed. In either case the radula is not used to envenomate the prey and is either used for further transportation in the oesophagus or for partial tearing of prey tissue.

The second sub-type is found in *Toxiclionella tumida* and differs from the first in that the buccal mass is located near the proboscis tip (Kantor, 1990, fig. 4), which has no distal sphincter. This species is characterized by a radula formed of hollow, and barbed marginal teeth (Kilburn, 1985, fig. 14), which are attached all along their length to the radular membrane. The hollow radular teeth are similar in morphology to those of higher conoideans. The gastropod has a long venom gland and in the posterior part of the proboscis there is a single salivary gland with paired ducts. The radular teeth are sufficiently long, that during protraction of the onto-

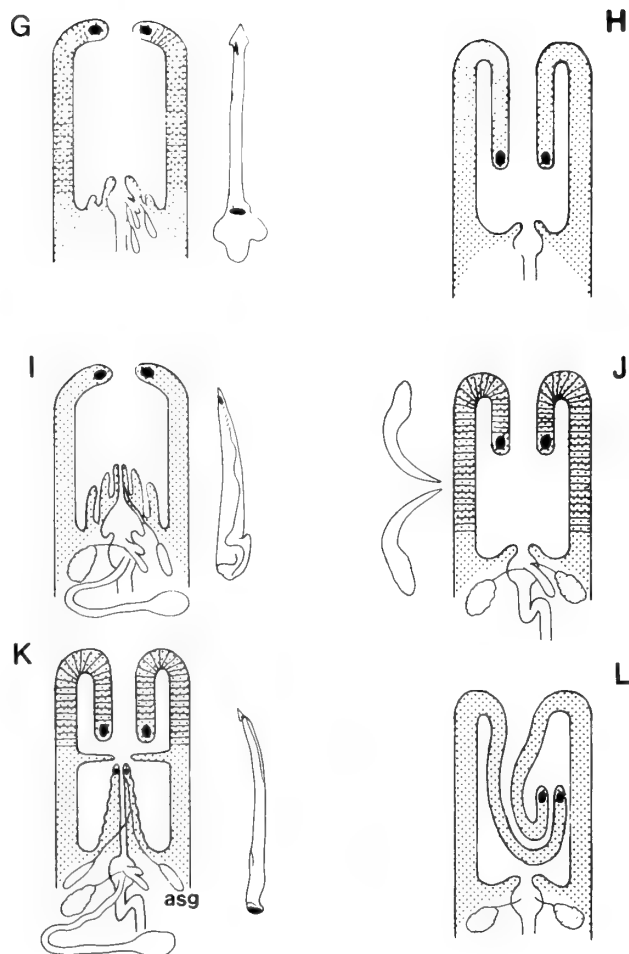


Fig. 26 Further types of foregut morphology found in the Conoidea. G. *Gymnobela emertoni*; H. *Philbertia linearis*; I. *Conus ventricosus*; J. *Duplicaria spectabilis*; K. *Terebra subulata*; L. *Terebra maculata*.

phore, the tips would protrude through the oral opening, and thereby stab the prey.

A comparable mechanism may occur in *Turricula nelliie spurius* (Taylor, 1985), which has the buccal mass located in a similar distal position in the proboscis to that of *T. tumida*, and during feeding can protrude the odontophore through the mouth opening (Miller, 1990). But *T. nelliie* possesses a sphincter in the anterior part of the buccal tube, and this feature usually correlates with the use of separate marginal teeth for stabbing (Kantor & Taylor, 1991).

In conclusion, we suggest that a similar type of feeding mechanism evolved independently in *Pseudomelastoma* and *Toxiclionella*. In the former, the primitive character of the radula suggests that the feeding mechanism is primary; whilst in *Toxiclionella* it is probably a secondary feeding mode when compared with other members of the subfamily. It is possible that with the shift of the buccal mass to the proboscis tip, *Toxiclionella* lost the mechanism of stabbing the prey with single marginal teeth and instead protrudes the radula through the mouth and uses the hollow teeth which remain firmly anchored to the radular membrane.

Feeding mechanism Type 2

The second feeding mechanism is typical of the majority of 'lower' turrids and the terebrid *Hastula bacillus*, which possess a well developed radular membrane and lack a radular caecum. The characteristic feature of this mechanism is the use of separate marginal teeth at the proboscis tip for stabbing the prey, whilst the radula is also used as a whole organ for different purposes (Sysoev & Kantor, 1986, 1989).

The use of single marginal teeth at the proboscis tip by turrids having radulas with well developed subradular membranes has been demonstrated in representatives of all 7 subfamilies of 'lower' Turridae (excepting the Pseudomelatominae) and also the terebrid *Hastula bacillus* (Kantor & Taylor, 1991).

According to the position of the buccal mass this type may be divided into two sub-types. Gastropods of the first sub-type have the buccal mass situated at the proboscis base. These include species of Drillinae, Cochlespirinae, Turrinae and many Crassispirinae. In these gastropods, the solid or wishbone marginal teeth, which become detached from the membrane during its degeneration in the sublingual pouch, are used at the proboscis tip for stabbing the prey. It should be noted, that separate teeth were not found in the sublingual pouch, therefore it does not serve for the storage of teeth. Meanwhile, the radula as a whole organ probably has a different function within the buccal cavity. This is most likely for the transport of food from the cavity to the oesophagus. Some evidence for this comes from the observations of Maes (1981), who noted the presence of intact sipunculans in the posterior part of the oesophagus of *Drillia cydia* (Drillinae). Although at first sight, it might be thought that the large, pectinate, lateral teeth found in this species might serve for tearing or rasping the prey.

A characteristic feature of the proboscis is the presence of the sac-like enlargement of the anterior part of the buccal tube and a well-developed, distal sphincter(s). Gastropods of this group lack a radular caecum, so they can use only teeth which are sporadically detached from the membrane. Either the marginal teeth are not used in every feeding act, or, the teeth are held at the proboscis tip for a long time. That is, from the moment of their detachment from the subradular membrane to the next feeding act. We have found teeth at the proboscis tip in sections of 'lower' turrids much more frequently, than in the 'higher' turrids. Moreover, in *Splendrillia chathamensis*, in addition to the normal buccal sphincters of the buccal tube, teeth are attached by their base to a 'mat' of epithelial cells in the enlargement of the buccal tube (Kantor, 1990, fig. 3). Such a mechanism of tooth fixation confirms the long-term presence of the tooth at the proboscis tip. Thus, the enlargement of the anterior part of the buccal tube, could be considered as a functional analogue of the radular caecum.

The use of marginal teeth at the proboscis tip, in turrids with a well-developed radular membrane, explains how hollow, marginal teeth might have evolved independently in different groups possessing the radular membrane and odontophore. For example, *Imaclava* (Drillinae) (Shimek & Kohn, 1981), has hollow teeth and most probably uses these at the proboscis tip for stabbing the prey in a manner similar to that of higher Conoidea.

The second feeding sub-type is seen in *Funa latisinuata* (Crassispirinae), which feeds upon nemerteans. From dissection of relaxed animals, Miller (1989, fig 6f) showed that in

the everted position, the buccal mass with the radula is protruded through the mouth opening (Fig. 14a). In sections of animals with a contracted proboscis, the buccal mass lies towards the base. It is known that this species uses the marginal teeth at the proboscis tip (Kantor & Taylor, 1991). Thus, the mode of feeding may be reconstructed as follows. After stabbing the prey, the gastropod everts the buccal mass, with the walls of the buccal tube, through the mouth opening and picks up the prey with the protruded radula. With retraction of the buccal mass, the prey is pulled into the proboscis. Correlated with this feeding mechanism, is the elongation of the anterior oesophagus between the buccal mass and the circum-oral nerve ring. During protraction of the buccal mass, the oesophagus should be pulled through the nerve ring. But, as the nerve ring in Conoidea is highly concentrated, and usually tightly attached to the oesophagus, the only possibility is the elongation of the oesophagus itself anterior to the nerve ring, forming a loop, which is straightened during eversion of the buccal mass (Fig. 14b).

In addition to *Funa latisinuata*, this elongation of the oesophagus between the buccal mass and the nerve ring has been found in species from several different subfamilies of Turridae-Pseudomelatominae, all Clavatulinae, *Pilsbryspira nympha* (Zonulispirinae), *Vexitomina* (Crassispirinae), *Turricula nelliiae spurius* (Cochlespirinae), the radulate terebrids, *Hastula bacillus*, and *Pervicacia tristis* (Pervicaciidae). It is likely, that the turrid species at least have a feeding mechanism similar to that of *F. latisinuata*. The elongation of the anterior oesophagus is usually associated with the permanent shifting of the buccal mass towards the distal end of the proboscis. This is well demonstrated in the Clavatulinae and probably facilitates the eversion of the buccal mass through the mouth.

In all species possessing an elongated oesophagus (except *Pseudomelatomina*), there is a change in the histology of the anterior part of the venom gland after its passage through the nerve ring. However, such a change occurs in two species (*Lophiotoma leucotropis* and *Inquisitor* sp.) which lack the elongated oesophagus. The anterior part of the gland is ciliated and duct-like, with no secretory granules. This indicates, that the differentiation of the gland is connected with the elongation of the oesophagus and thus, the latter is a secondary feature.

Feeding mechanism Type 3

The majority of Conoidea possess the third type of feeding mechanism, in which separate marginal teeth are used at the proboscis tip for stabbing prey, and the radula not used as a whole organ.

The very specialized radular morphology is the most remarkable and well-known feature of the toxoglossan digestive system. It is characterized by a marked tendency towards a reduction in the strength of the subradular membrane, leading to its complete absence in many species of Turridae, the majority of Terebridae and all Conidae. Species without a subradular membrane, have a radula consisting only of complex, hollow, marginal teeth. They are known for the highly specialized feeding mechanism, in which individual teeth are used at the proboscis tip for stabbing and killing prey with secretions of peptide neurotoxins produced by the venom gland (Oliviera *et al.* 1990).

Despite the similarities with the previous feeding mechanism, those 'higher' conoideans with hollow teeth and no

radular membrane are extremely diverse compared with the 'lower' conoideans. Moreover, this relative diversity has steadily increased throughout the Cenozoic (Sysoev, 1991). This suggests that higher conoideans may possess some adaptive advantages. In our opinion these advantages lie in the features of the morphology of the radular diverticulum.

The higher Conoidea lack a subradular membrane, and the radular diverticulum is divided into two different parts; the radular sac and radular caecum (also known as long and short arms). The caecum serves for the storage of the fully-formed, marginal teeth. Many teeth can be stored; for example, in a specimen of *Mitromorpha* (*Mitrolumna*) sp. there were 106 teeth in the radular sac compared with 64 in the caecum (Kantor & Sysoev, 1990). Species of higher Conoidea can probably use several teeth in each feeding act. For example, observations on the feeding of *Conus textile* showed that up to 17 teeth can be used in the same attack (Schoenberg, 1981). By contrast, in lower turrids, there is no caecum and probably no more than a single tooth can be used in each feeding act. Predatory attacks by higher Conoidea are thus likely to be more successful, and the mechanism of prey capture probably more efficient. This may explain the relative success of the higher Conoidea.

The feeding and diets of gastropods of this functional type are well known (Oliviera *et al.* 1990) and it is unnecessary to describe the process in detail. Only the most important morphological features should be noted. These are the vestigial, or completely reduced, radular membrane; the absence of an odontophore; the presence of a radular caecum where the fully-formed marginal teeth are stored, and a well-developed oral sphincter for gripping the teeth. The radula is represented by hollow, marginal teeth. The tooth ligament (long flexible stalk attached to the tooth base) is probably the rudiment of the radular membrane (Fig. 23c). Also the gastropods of this group often have enlarged rhynchostomal lips. In some species, the lips are able to invert (i.e. to form an introvert or pseudoproboscis) and this is also used in prey capture. It should be noted, that some vermivorous species of *Conus* (Marsh, 1970) and the fish-feeding *C. geographus* (Johnson & Stabulum, 1971) do not stab they prey in every feeding act. This is possibly an initial stage of transition to feeding mechanism type 5.

Usually, teeth are gripped at the proboscis tip by the buccal tube sphincter, but in some turrids the buccal tube introvert (valvule of Sheridan *et al.*, 1973) is involved (Fig. 9). This structure has been reported so far in *Mangelia nebula* (Sheridan *et al.*, 1973; Delaunoy & Sheridan, 1989) and in *Eucithara stromboides* (Fig. 10). It is also possible, that the buccal tube introvert can be everted through the mouth opening and have a role in holding the prey.

After envenomation, the prey may be held by the tooth itself, as occurs in many vermivorous species of *Conus* (Kohn, 1959), or with the mouth. The buccal lips may play a role in the transport of prey to the buccal cavity. These are highly protrusive in many Mangeliinae, and at least in *M. nebula* (Fig. 9) can be retracted into the buccal cavity (Delaunoy & Sheridan, 1989). A similar possibility was described for *Oenopota* by Bogdanov (1990), who suggested that the buccal lips and the proboscis itself might be inverted into the buccal cavity.

II. Venom gland absent

Feeding mechanism Type 4

Gastropods of this group have a radula with a well-developed radular membrane and a proboscis may be either present or reduced. According to the position of the buccal mass they can be divided into two sub-types.

Conoideans of the first sub-type which at present includes only *Strictispira* and probably *Cleospira*, have the buccal mass located at the tip of a well-developed proboscis (Fig. 13). The buccal mass and radular apparatus are large, with two large odontophoral cartilages and massive odontophoral and proboscis retractor muscles. The radula has a strong membrane with two rows of solid, awl-shaped, marginal teeth. The buccal tube is very short and there are no oral sphincters. Apart from the record of polychaete setae in two individuals of *Strictispira paxillus* (Maes, 1983), nothing is known of the habits of this group.

The terminal position of the buccal mass on the muscular proboscis, the short buccal tube and the massive radular apparatus, suggest that when the gastropod is feeding the radula is protracted out of the extended proboscis tip. The solid teeth and absence of venom apparatus suggest that the radula is involved in biting and tearing rather than stabbing. The feeding mechanism is thus probably more similar to other neogastropods such as the Buccinidae rather than to other conoideans.

Conoideans of the second sub-type differ from these of the first one in possessing a basal buccal mass. The radula is well-developed, whilst the proboscis is either absent or highly reduced, and a rhynchostomal introvert is usually present. This feeding mode is found in the Pervicaciidae. The diet of this family is largely unknown, except for '*Terebra*' *nassoides* which feeds on capitellid polychaetes (Taylor, 1990).

In the Pervicaciidae, the absence of a proboscis means that the rhynchodeal introvert becomes the main organ of prey capture, as occurs in some proboscis-less terebrids such as *T. gouldi* (Miller, 1975). Prey are presumably pulled into the rhynchocoel by the introvert. In *Duplicaria spectabilis* there are large muscular buccal lips and probably a protrusive odontophore (Taylor, 1990, fig. 7). However, in *Pervicacia tristis* and *Duplicaria kieneri* there is a septum with a narrow aperture dividing the rhynchocoel and it is very unlikely that the odontophore can be protruded through the septum. Although we have no direct evidence, it is possible that the septum functions to hold prey during swallowing and perhaps early digestion.

Feeding mechanism Type 5

Finally, there are many conoideans which lack a radula, venom and salivary glands. Gastropods of this group include some Daphnellinae, Taraninae and some Terebridae. In addition to the absence of foregut glands and radula, a characteristic feature of these species is the very reduced size or complete absence of the proboscis. Radula-less Conoidea either have well-developed, rhynchostomal lips or a large rhynchostomal introvert, as for example, in the Terebridae (Miller, 1975) or *Philbertia linearis* (Sheridan *et al.*, 1973). It is possible, that a rhynchostomal introvert is also present in *Teretiopsis*, although all sectioned specimens have it in the extended position and it was overlooked during the original description (Kantor & Sysoev, 1989). In some turrids, such as

Cenodagreutes (Smith, 1967) and *Abyssobela atoxica* (Kantor & Sysoev, 1986), which lack the rhynchodeal introvert, there is a vast rhynchocoel and well-developed cavity between the rhynchodaeum and body walls. The walls of this cavity are connected by numerous transverse muscles. Both the introvert and cavity are lacking in the genus *Taranis* (Taraninae).

A feeding mechanism for radula-less species is known for some terebrids (Miller, 1970, 1975). Thus, *Terebra gouldi* which has a relatively short introvert feeds upon the enteropneust *Ptychodera flava*, and *Terebra maculata* with a long introvert feeds on polychaetes. Prey are caught with the aid of the introvert. Turrids lacking the introvert, but with the cavity between the rhynchodaeum and the body walls, probably engulf prey by contraction of the radial muscles in the wall. This would cause negative pressure and an increase in the inner volume of the rhynchocoel.

The origin of the radula-less feeding mechanism can be easily envisaged. It is known, that in some *Conus* species hypodermic envenomation is not necessary in each feeding attack (Kohn, 1959; Marsh, 1970; Sanders & Wolfson, 1961). It is probable that some Turridae and Terebridae, especially those with well-developed rhynchostomal lips or introvert, also feed without stabbing the prey with radular teeth. Thus, *Daphnella reeveana*, which possesses a venom gland, has a very short proboscis and is probably unable to hold a tooth at its tip (Fig. 4). As stabbing of the prey becomes unnecessary, the proboscis, venom gland and radula disappear. An intermediate stage is found in *Gymnobela emertoni*, in which the proboscis and venom gland have disappeared, but there is still a very short and reduced radular sac, opening to the outer side of the buccal lip (Fig. 8).

RELATIONSHIPS OF THE CONOIDEA

Monophyly of the Conoidea

There has been much discussion concerning the relationships of the Conoidea to other prosobranch gastropods; some considering them to be part of a monophyletic group with other neogastropods (Ponder, 1973; Taylor & Morris, 1988), whilst others suggest an origin entirely independent of the neogastropods (Sheridan *et al.* 1973; Shimek & Kohn, 1981; Kantor, 1990).

In this section we briefly review some of the evidence for the relationships of the Conoidea with other prosobranchs. Some of this evidence has been discussed in some detail by Kantor (1990) and only the principal arguments are presented here.

The location of the buccal mass at the base of the proboscis as found in most conoideans, is different from the situation seen in most neogastropods, where the buccal mass is found at the distal end of the proboscis. The proboscis in most conoideans is formed by the elongation of the buccal tube, whilst in neogastropods it originates from the elongation of the anterior oesophagus (Ponder, 1973). However, a basal buccal mass is now known for the neogastropod *Benthobia* (Pseudolividae) which also exhibits a number of other primitive characters, and in *Amalda* (Olividae) (Kantor, 1991). Additionally, in *Benthobia*, the radular retractor muscle passes through the nerve ring and is connected to the columellar muscle (Kantor, 1991 fig. 15a). This condition is seen species of the turrid subfamily Drillinae, and in most

lower caenogastropods, but is absent in probosciform caenogastropods.

A key autapomorphy of the Conoidea is the possession of the venom apparatus, comprising the venom gland and muscular bulb. There has been much discussion concerning the homology of this gland. But, Ponder (1970; 1973) showed, that in the neogastropod family Marginellidae a long coiled gland, similar in general appearance to the conoidean venom gland is formed by the stripping off of glandular folds from the oesophagus. In some marginellids the gland terminates at the posterior in a muscular bulb which is homologous with the gland of Leiblein. The venom gland of conoideans may have been derived in a similar way and is probably homologous with the glandular folds of the oesophagus and the gland of Leiblein in other neogastropods.

The possession of tubular, accessory salivary glands is also considered to be an apomorphy of the Neogastropoda (Ponder, 1973). These glands are patchily distributed amongst conoideans, but are known in some Turridae, Conidae and Terebridae. Both the histology of the glands (Schultz, 1983; Andrews, 1991) and the position of the opening of the ducts, confirms their homology in the Conoidea and in other neogastropods. The primitive *Benthobia* also has a large accessory salivary gland (Kantor, 1991).

A radula with five teeth in each row, as is found in the turrid subfamily Drillinae, has been considered as evidence for a separate origin of the Conoidea and Neogastropoda, the latter normally have three or less teeth in each row. (Shimek & Kohn, 1981). However, it is now known that some *Olivella* and Nassariidae have five teeth in each row (Bandel, 1984; Kantor, 1991). All this suggests is that the common ancestor of the Conoidea and the other neogastropods possessed five or more teeth in each row.

In conclusion, conoideans share a number of characters with the neogastropods which suggest a common ancestry. Nevertheless, the evidence both from the position of the buccal mass and the formation of the proboscis, suggests an early divergence of the two groups. An evolutionary scheme for the derivation of the conoidean intraembolic proboscis from the acembolic type, typical of many mesogastropods, has been developed by Kantor (1990). His arguments corroborate and elaborate Ponder's (1973) hypothesis that the Conoidea diverged from the other neogastropods before the formation of the proboscis. Ontogenetic studies of proboscis and foregut development in the Conoidea and other neogastropods might provide corroborative evidence.

Relationships within the Conoidea

Phylogenetic analysis

We attempted to determine relationships within the Conoidea using cladistic analysis of many of the foregut characters described in the first part of this paper, combined with a few shell characters.

Taxa used

We have included 40 species in the analysis, with at least one from all the currently-recognised, subfamilies. In a few cases we have used previously published work. The species studied represent only a small proportion of living species from any of the subfamilies. Some of these subfamilies are very diverse and morphologically disparate and our sample is certainly

Table 2. Characters and character states of the foregut and shell used in cladistic analysis. See text for details of foregut characters.

* denotes characters where the states were treated as unordered.

Foregut characters

1.	Rhynchodeal introvert	0 — absent, 1 — present
*2.	Rhynchodeal sphincter	0 — present anterior, 1 — present posterior, 2 — absent
3.	Accessory proboscis structure	0 — absent, 1 — present
4.	Proboscis	0 — present, 1 — absent
5.	Transverse muscles in rhynchodeum wall	0 — absent, 1 — present
6.	Epithelium of posterior rhynchodeal wall continuous with proboscis wall	0 — absent, 1 — present
*7.	Sphincter at distal end of buccal tube	0 — absent, 1 — one sphincter, 2 — two sphincters
8.	Sphincter in middle of buccal tube	0 — absent, 1 — present
9.	Sphincter at base of buccal tube	0 — absent, 1 — present
10.	Buccal tube introvert ('valvule')	0 — absent, 1 — present
11.	Protrusive lips of buccal tube	0 — absent, 1 — present
12.	Position of buccal mass	0 — basal, 1 — distally shifted
13.	Connection of radular retractors to columellar muscle	0 — present, 1 — absent
14.	Extensible buccal lips	0 — absent, 1 — present
15.	Septum dividing anterior and posterior areas of the rhynchocoel	0 — absent, 1 — present
16.	Elongation of oesophagus between buccal mass and nerve ring	0 — absent, 1 — present
17.	Salivary glands	0 — two/one glands present, 1 — glands absent
18.	Salivary ducts	0 — two ducts present, 1 — one duct present
19.	Type of salivary gland	0 — acinous, 1 — tubular
20.	Accessory salivary glands	0 — two/one glands present, 1 — glands absent
21.	Radula	0 — present, 1 — absent
22.	Radular caecum	0 — absent, 1 — present
*23.	Central tooth	0 — robust muriciform, 1 — narrow 2 — broad with central spine
24.	Lateral teeth	0 — comb-like, 1 — absent
25.	Marginal teeth	0 — solid, 1 — wishbone, 2 — hollow, 3 — absent
*26.	Type of solid radular teeth	0 — flat, 1 — curved-pointed, 2 — semi-enrolled (<i>Hasula bacillus</i>)
*27.	Type of wishbone teeth	0 — large blade, small accessory limb, 1 — short knife type, equilimbed
*28.	Type of hollow teeth	0 — large base, 1 — thin small base
29.	Venom gland	0 — present, 1 — present with changed histology in anterior portion, 2 — absent
*30.	Connective tissue layer of muscular bulb	0 — present, 1 — absent
*31.	Muscle layers of muscular bulb	0 — more or less equal, 1 — outer layer thin, 2 — single layer only
32.	Odontophore	0 — present, 1 — absent
33.	Odontophoral cartilages	0 — not fused, 1 — fused

Shell and opercular characters

*34.	Shell form	0 — fusiform, 1 — coniform, 2 — turreted, 3 — terebriform, 4 — rounded
*35.	Number of protoconch whorls	0 — less than two, 1 — more than two
*36.	Sculpture of the protoconch	0 — absent or very weak, 1 — present
*37.	Siphonal canal	0 — not differentiated, 1 — moderate, 2 — long
*38.	Position of the anal sinus	0 — sutural, 1 — shoulder, 2 — peripheral, 3 weak or absent
39.	Presence of apertural ornament (teeth on the outer lip)	0 — absent, 1 — present
*40.	Number of the teleoconch whorls	0 — less than 4, 1 — from 4 to 8, 2 — more than 9
*41.	Development of subsutural ramp	0 — absent, 1 — present
42.	Operculum	0 — present, 1 — absent
43.	Position of opercular nucleus	0 — terminal, 1 — mediolateral

inadequate. Although anatomical data are available for many terebrids (Taylor, 1990 and unpublished), most of these were eventually excluded from the analysis for the following reason. Many of the morphological trends in the Terebrinae, involve partial to total loss of the foregut organs (Taylor, 1990); thus many of the characters used in the cladistic analysis were recorded as missing. In our earlier attempts at cladistic analysis, terebrid species tended to appear in rather disparate positions on the cladograms. Consequently, we have used only three species to represent the Terebrinae and

Pervicaciinae, the taxa being the least-derived known for each group.

Characters

We used 43 characters, coded as 101 states in the analysis. Of these, 35 characters concerned foregut anatomy and a further eight, the shell or operculum. The characters and their states are listed in Table 2. Full discussion of the anatomical characters will be found in the section of this paper concern-

Table 4. Synapomorphies for interior nodes. Nodes numbered as in Fig. 27.

Node	Synapomorphies (Character: state)
1	7(1), 20(1), 35(0), 37(0), 38(1)
2	13(1), 23(2), 24(1), 26(1)
3	1(1), 3(1), 34(3), 38(3), 40(2)
4	4(1), 14(1), 15(1), 29(1)
5	25(1), 37(1)
6	6(1), 16(1), 41(1)
7	7(0), 23(0), 25(0)
8	12(1)
9	33(1), 43(1)
10	7(2), 29(1)
11	12(1)
12	34(0), 40(0)
13	14(1), 27(0), 43(0)
14	7(1), 35(1)
15	
16	34(0), 37(2)
17	2(1), 38(2), 40(2)
18	22(1), 25(2), 32(1)
19	
20	20(0)
21	2(1), 34(0)
22	2(1), 14(1), 28(0)
23	18(1)
24	14(0), 35(1), 39(1), 42(1)
25	7(1), 35(1)
26	8(1), 34(0)
27	20(0), 39(0)
28	19(1), 36(1)
29	28(0), 42(1)
30	10(1), 11(1)
31	6(1), 7(1), 14(1), 31(1)
32	30(1), 31(2), 38(0)
33	1(1), 14(1), 21(1), 39(1)
34	38(3)
35	4(1)
36	5(1), 29(2), 39(0), 41(1)
37	17(1), 40(0)
38	1(0), 35(0)

which are the only conoideans possessing five teeth in each radular row. They also retain the connection of the radular retractor muscle to the columellar muscle. Their distinctive apomorphy is the possession of large, comb-like lateral teeth. We have studied only three species in this group (the third species identical to *Clavus unizonalis*) which are very similar to each other. However, we note the very different hollow, enrolled 'hypodermic-style' marginal teeth of *Imaclava* (Shimek & Kohn, 1981) and the possible 'wishbone' marginals of *Drillia roseola* (McLean, 1971). Anatomical studies of these taxa are needed to determine their status.

All other conoideans are separated from the Drilliidae at Node 2 by the loss of the radular retractor/columellar muscle connection, by the loss of the lateral teeth and possession of curved pointed marginal teeth. None of the non-drilliid taxa that we have included in the cladistic analysis possess lateral teeth, although what appear to be vestigial lateral teeth are seen for example in *Antiplanes* (Kantor & Sysoev, 1991) and a few other species. Also, it is possible that the broad central teeth seen in Cochlespirinae may be formed by fusion of lateral teeth. Another apomorphy at this node is the possession of a broad central tooth with a spine-like central cusp.

Node 3 separates the Terebridae, with five apomorphies including the possession of a rhynchodeal introvert and the accessory proboscis structure. The Perviciacinae (Node 4) are separated from *Hastula* (representing the Terebrinae) by the loss of the proboscis, the presence of extensible buccal lips, a septum in the rhynchocoel (although this is present in some Terebrinae) and the loss of the venom gland.

Node 5 separates all other conoideans with two apomorphies namely the presence of wishbone marginal teeth and a moderately long siphonal canal. The latter is a weak character and although we consider the former to be a strong character, some taxa in Clade 6 have solid teeth which PAUP considers a reversal from the wishbone condition.

Clade 6 comprises taxa with the epithelium of the posterior part of the rhynchodeum continuous with that of the proboscis and with an elongated loop of oesophagus anterior to the nerve ring.

Clade 7 includes two taxa with solid marginal teeth and no buccal tube sphincter and *Toxiclionella* which has hollow teeth. PAUP treats the solid teeth as a reversal, but we think that this is unlikely. However, it is possible that the 'flanges' on the teeth of Strictispirinae may be modifications of a second limb on the tooth. *Toxiclionella* and *Strictispira* are grouped together at Node 8, because both have a buccal mass situated at the distal end of the proboscis. However, *Toxiclionella* shares many characters with the Clavatulinae (including the medio-lateral nucleus of the operculum), but has a very different radula with hollow and barbed marginal teeth firmly attached to the radular ribbon located in the distal buccal mass. Although *Toxiclionella tumida* lacks a central tooth, a clavatuline type central is known in *T. elstoni* (Kilburn, 1985). *Turricula nelli* (Node 12) shares many apomorphies with clavatuline species and should be transferred from the Cochlespirinae to the Clavatulinae.

PAUP suggests that *Funa* and *Vexitomina* (Crassispirinae) and *Pilsbryspira* (Zonulispirinae) are derived from the Clavatulinae. They share a number of characters, but *Funa* and *Vexitomina* have distinctive wishbone teeth with one broad flat limb and a small, thin, subsidiary limb. *Pilsbryspira* has enrolled marginal teeth and a distal buccal mass. This type of tooth could be derived by enrollment of the crassispirine type of wishbone tooth. Both groups have an operculum with a terminal nucleus which PAUP treats as a reversal from the medio-lateral nucleus of the Clavatulinae.

Lophiotoma and *Polystira* (Turrinae) (Node 16) have a peripheral anal sinus and a posteriorly situated rhynchodeal sphincter. *Aforia* has an accessory salivary gland and PAUP treats this appearance as a reversal, the glands having already been lost between the outgroup and the first node. However, it is highly unlikely that these glands are regained once lost. Accessory glands have a very patchy distribution amongst the Conoidea (*Conus*, *Benthofascis* and some Clathurellinae) and apart from their occurrence in some terebrids, *Aforia* is the only 'lower' conoidean in which we have seen the glands. The distribution of this character should become clearer as more species are examined. Maybe significant, is the fact that *Aforia* is the only other conoidean in which the multidigitate osphradial leaflet typical of *Conus* has been found (Sysoev & Kantor, 1988 fig. 2J).

From Node 18 onwards are all the so-called 'higher' conoideans, which in all our analyses form a monophyletic group. The apomorphies which define this node are the presence of a radula caecum for storage of detached radular teeth, hollow, enrolled marginal teeth, loss of the radular

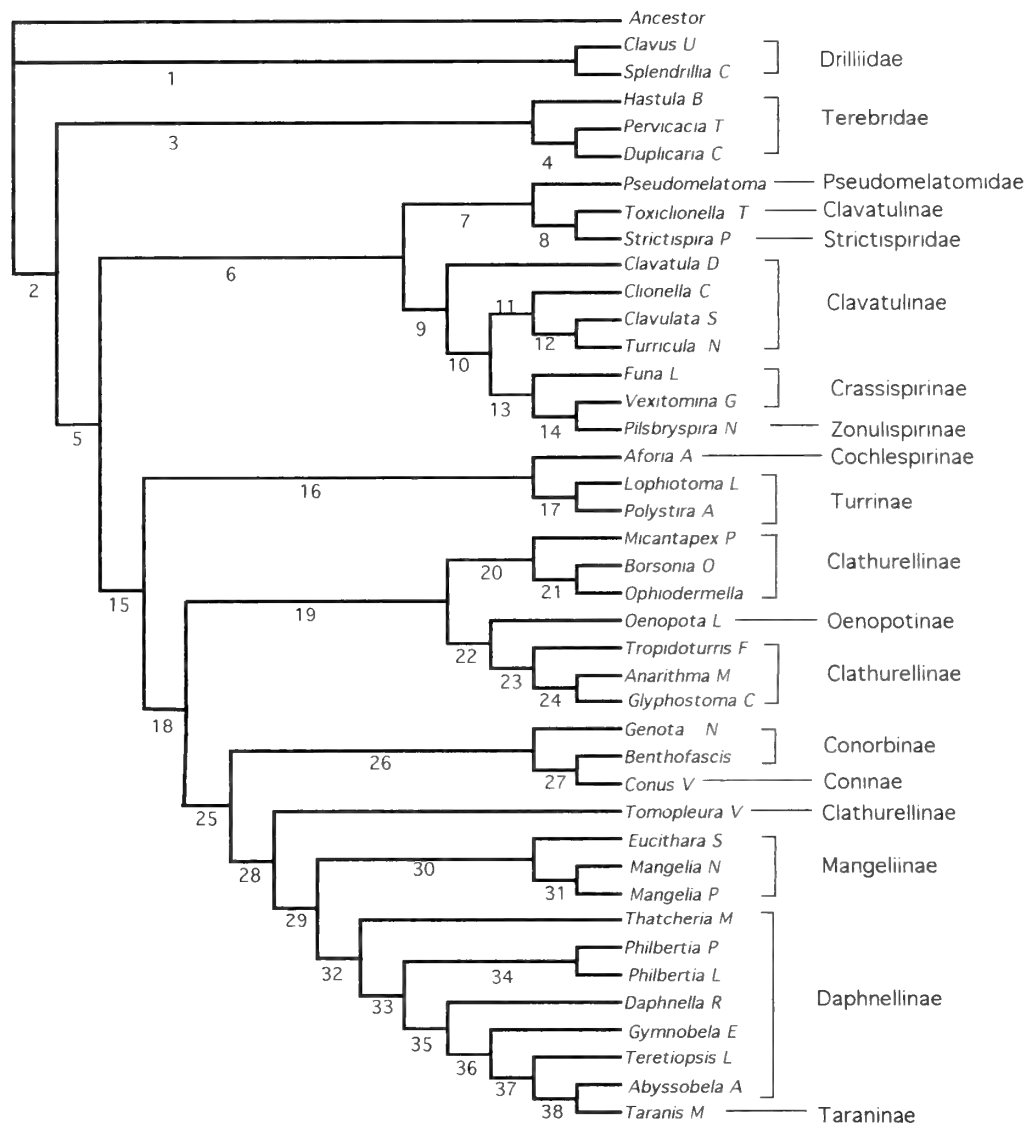


Fig. 27 Majority-rule (50%) consensus tree. Autapomorphies for each node given in Table 4. Higher taxa names at the top of branches reflect our new classification. Taxon abbreviations in order top to bottom on the tree: *Clavus U* = *Clavus unizonalis*, *Splendrillia C* = *Splendrillia chathamensis*, *Hastula B* = *Hastula bacillus*, *Duplicaria C* = *Duplicaria colorata*, *Pseudomelatomata P* = *Pseudomelatomata penicillatus*, *Toxiclionella T* = *Toxiclionella tumida*, *Strictispira P* = *Strictispira paxillus*, *Clavatula D* = *Clavatula diadema*, *Clionella S* = *Clionella sinuata*, *Clavatula C* = *Clavatula caerulea*, *Turricula N* = *Turricula nelliae*, *Funa L* = *Funa latisinuata*, *Vexitomina G* = *Vexitomina garrardi*, *Pilsbryspira N* = *Pilsbryspira nympha*, *Aforia A* = *Aforia abyssalis*, *Lophiotoma L* = *Lophiotoma leucotropis*, *Polystira A* = *Polystira albida*, *Micantapex P* = *Micantapex parengonius*, *Borsonia O* = *Borsonia ochraea*, *Ophiidermella I* = *Ophiidermella inermis*, *Oenopota L* = *Oenopota levidensis*, *Tropidoturris F* = *Tropidoturris fossata*, *Anarithma M* = *Anarithma metula*, *Glyphostoma C* = *Glyphostoma candida*, *Genota N* = *Genota nicklesi*, *Benthofascis* = *Benthofascis biconica*, *Conus V* = *Conus ventricosus*, *Tomopleura V* = *Tomopleura reevei*, *Eucithara S* = *Eucithara stromboides*, *Mangelia N* = *Mangelia nebulosa*, *Mangelia P* = *Mangelia powisiana*, *Thatcheria M* = *Thatcheria mirabilis*, *Philbertia P* = *Philbertia purpurea*, *Philbertia L* = *Philbertia linearis*, *Daphnella R* = *Daphnella reeveana*, *Gymnobela E* = *Gymnobela emertoni*, *Teretiopsis L* = *Teretiopsis levicarinaratus*, *Abyssobela A* = *Abyssobela atoxica*, *Taranis M* = *Taranis moerchi*.

ribbon and loss of the odontophore.

Clade 19 is made up of various taxa formerly included in the Borsoniinae and Clathurellinae with the addition of *Oenopota* (Oenopotinae). The apomorphies defining the nodes are very unsatisfactory with many reversals. More characters need to be analysed in these taxa to achieve better resolution.

Borsonia and *Ophiidermella* (Node 21) have posteriorly situated rhynchodeal sphincters, and fusiform shells. The

taxa in the other clade (Node 22) have extensible buccal lips and hollow radular teeth with large bases. Although the Oenopotinae have been previously thought to have close affinities with the Mangeliinae, they do have acinous salivary glands, rather than the tubular type associated with the latter subfamily.

A clade comprising *Anarithma* and *Glyphostoma* is defined (Node 24) by three characters; a posteriorly situated rhynchodeal sphincter, a single salivary duct and apertural orna-

ment. *Glyphostoma* has long slender radular teeth and has been separated in the family Clathurellinae (McLean, 1971). *Anarithma* has been classified in the Diptychomitridae (= Mitrolumninae), but Kilburn (1986) could see no significant differences from the Borsoniinae.

Taxa normally classified in the Borsoniinae (*Ophiodermella*, *Borsonia*, *Tomopleura*, *Micantapex*, *Tropidoturris* and *Anarithma*) do not form a monophyletic group in any of our analyses. For this reason, in the classification derived from this study we are leaving these taxa, along with *Glyphostoma* and others in informal groupings within the subfamily Clathurellinae.

Benthofascis (Conorbinae) and *Conus* (Coninae) (Node 27) share a number of characters. They lack an anterior sphincter to the buccal tube, but have have an intermediate sphincter instead. Both have accessory salivary glands and retain an operculum. Additionally, both genera show resorption of the inner shell whorls. Although *Genota* (Node 26) is usually classified in the Conorbinae, it lacks an operculum.

Taxa from Node 28 onwards have tubular salivary glands and most have sculptured protoconchs. The Mangeliinae (Node 30), represented by *Eucithara* and *Mangelia*, are a well-defined group with the distinctive buccal tube introvert, and protrusive lips of the buccal tube. Taxa from Node 32 have a muscular bulb made up of only one muscle layer and lacking the connective tissue layer, with additionally, an anal sinus located at the suture. *Thatcheria* (Node 32) has many characters in common with the Daphnellinae and until many more daphnellines have been examined anatomically it can be classified with them. However a great range of foregut anatomy is found in the Daphnellinae and it may be that the group is paraphyletic. At the extreme end of the tree (Node 36) are taxa which have lost many foregut characters such as radula, proboscis and glands. *Taranis* has been classified in a separate subfamily Taraninae (Kantor & Sysoev, 1989), but it has so few characters that its relationships are obscure. It may be a highly derived daphnelline.

Conclusions

Our studies have shown that several major autapomorphies associated with the Conoidea have developed independently in separate clades. Also there has been parallel loss of foregut structures. Some of the more important of these are briefly discussed below.

Hollow, enrolled 'hypodermic style' radular teeth are considered a distinctive feature of the conoidean feeding mechanism. Our analysis shows that hollow teeth have been independently derived at least five times in the evolution of the Conoidea. In *Imaclava* the hollow marginal teeth seem to have developed from the enrolling of the flattened drilline-type of marginal teeth. In *Toxiclionella*, the hollow teeth were derived from wishbone teeth similar to those of *Clavatula* or maybe from solid teeth like those of *Pseudomelasma*. Hollow teeth are found in many Terebridae and are thought to have been derived from solid teeth via semi-enrolled intermediate forms such as found in *Hastula bacillus*. The enrolled teeth of *Pilsbryspira* (Zonulispirinae) may have been derived by enrolling of the crassispirine type of wishbone tooth. The hollow teeth of the higher conoideans such as Clathurellinae, Coninae, Mangeliinae and Daphnellinae in all their various forms may represent another separate derivation. The radular caecum found in some Terebridae was derived independently of that found in the higher turrids

(Clathurellinae, Oenopotinae, Mangeliinae, Daphnellinae) and Coninae.

The rhynchodeal introvert found in some Daphnellinae, is also found in all Terebridae (including perricaciines). If our ideas concerning the relationships of the Terebridae are correct, then the structure was evolved independently in the two groups.

A buccal mass situated at the base of the proboscis is considered to be a diagnostic character of the Conoidea (Ponder, 1973). However, in *Turricula nelliae* the buccal mass was shown to be located at the distal end of the proboscis (Taylor, 1985; Miller, 1990). We now know that a distally-shifted buccal mass seems to be common feature of the Clavatulinae and is found also in *Pilsbryspira* (Zonulispirinae) and *Strictispira* (Strictispirinae) which lacks the venom apparatus.

One surprising trend seen in at least four clades is the loss of the venom apparatus. In the Daphnellinae, Taraninae and some Terebrinae this is associated with the loss of the proboscis and radular apparatus. Perricaciinae have a well developed radula apparatus but no proboscis or venom gland. By contrast, *Strictispira* which also lacks the venom gland, has a proboscis, a distally-located buccal mass and a robust radula apparatus.

Relationships and status of Terebrinae and Perricaciinae

Some controversy concerns the status of the Terebrinae and Perricaciinae. Rudman (1969) and Taylor (1990) suggested an independent origin for the two groups. However, anatomical studies of more species is revealing some shared apomorphies which suggest a common origin.

Although both subfamilies possess elongate multi-whorled shells there are large anatomical differences between the two groups. The family Perricaciidae was originally proposed by Rudman (1969) for *Perricacia tristic*, a terebriform species with no proboscis and venom apparatus, but with an odontophore and a radula with a strong membrane and two sickle-shaped, solid teeth in each row. It is now known, that many more 'terebrids' (*Duplicaria* species and others) share these characters and should be included in the family (Taylor, 1990). Other characters of perricaciids include a rhynchodeal introvert and a septum in some species.

Most of the radulate Terebrinae s.s. possess hollow and barbed, radular teeth, similar to those seen in *Conus* and the Clathurellinae. However, some *Hastula* species possess an odontophore and *Hastula bacillus* has partially-solid teeth (Taylor & Miller, 1989). This discovery demonstrates that the Terebridae must be derived from a lower conoidean with an odontophore and radular ribbon, rather than from some group such as the Clathurellinae, which have lost these structures.

The accessory proboscis structure is an unusual organ found in some Terebrinae, and is known from *Hastula bacillus*, *H. aciculina*, *H. imitatrix*, *H. raphanula*, *Terebra affinis* and *T. pertusa* (Miller 1971, Taylor, 1990; Auffenberg & Lee, 1988; Taylor, unpub.). Some terebrines, for example *Terebra subulata*, also possess a septum dividing the rhynchocoel (Miller, 1971; Taylor 1990). We have found an accessory proboscis structure in the western Australian species *Duplicaria kieneri*, and *Duplicaria colorata* (recently described as a *Hastula* by Bratcher (1988)), which otherwise

have an anatomy similar to *Pervicacia*.

Although the pervicaciines and terebrines apparently differ considerably in foregut anatomy, they share a number of characters which suggest a common origin (Table 5). The idea that the Terebrinae and Pervicaciinae were derived separately (Rudman, 1969; Taylor, 1990) is rejected. Characters in common between the two groups are: the elongate multi-whorled shell, the rhynchodeal introvert, and in some species the rhynchodeal septum and accessory proboscis structure. Thus, we propose that the common ancestor of the combined Pervicaciinae and Terebrinae clade would have possessed a rhynchodeal introvert, a proboscis, an odontophore, a radula with two solid, sickle-shaped, marginal teeth in each row, a venom gland, a pair of acinous salivary glands, a pair of accessory salivary glands, an accessory proboscis structure and a rhynchodeal septum.

Species in the Pervicaciinae clade have lost the proboscis, venom gland and accessory salivary glands. In the Terebrinae clade, the solid radular teeth were transformed into semi-enrolled and then hollow teeth. The odontophore was also progressively lost. Species with hollow teeth have developed a radular caecum. Other, more-derived terebrines and possibly pervicaciines, have lost virtually all the foregut structures, with the rhynchodeal introvert becoming the main feeding organ (Taylor, 1990).

Because the radula with solid, sickle-shaped marginal teeth and well developed odontophore, is regarded as one of the least-derived for the Conoidea, we regard the Pervicaciinae/Terebrinae clade as an early branch from the rest of the Conoidea. If our hypothesis of relationships is correct, then the hollow, barbed teeth, the radular caecum, the rhynchodeal introvert, and rhynchodeal septum of the terebrids, have been derived independently of those similar structures found in the Daphnellinae and Clathurellinae.

Status of Conidae

Despite the distinctive shell form and high species diversity of the group, we have little anatomical evidence to support the separation of *Conus* at family-level from other higher turrids. We propose only sub-family status for the group. Every anatomical character-state of the conine foregut is shared with species of Clathurellinae and Conorbinae. Some *Conus* species possess a snout gland in the rhynchocoel, but this

organ has been little studied. *Conus* species also have a distinctive osphradium with the multidigitate leaflets (Taylor & Miller, 1989). However, the detailed structure of the osphradium has been studied in only a few species of Turridae, but at least in some *Aforia* species (Cochlespirinae) there are similar digitate osphradial leaflets (Sysoev & Kantor, 1988). The resorption of the inner shell whorls has been used as a diagnostic character of conines (Kohn, 1990), but the occurrence of this feature has been little studied in other conoideans, although it is present in *Benthofascis* (Conorbinae).

CLASSIFICATION OF CONOIDEA

Introduction

Although many of the subfamilial names (as well as apparent synonyms) currently-used within the Turridae were introduced in the 19th or early 20th century, no detailed and well-documented classification was developed in these earlier works. Most authors based their classifications exclusively on shell characters, although Stimpson (1865) used radula data and Fischer (1887) divided the Conoidea into four subfamilies solely by opercular characters. The rather detailed classification of Casey (1904) who recognised eight tribes within the Turridae (Donovaniini are not conoideans), was based on both opercular and shell characters.

Thiele (1931) classified turrids into three subfamilies contained within the family Conidae, with the Terebridae as a separate family. Diagnoses of the turrid subfamilies mainly consisted of combinations of such characters as 'operculate-inoperculate' and 'toxoglossate-nontoxoglossate dentition'. This was the first classification where the taxonomic difference between toxoglossate and nontoxoglossate radulae was definitely indicated. An elaboration of this classification was developed by Wenz (1938) who recognised five subfamilies of Turridae as well as the Conidae and Terebridae.

The classification of Powell (1942, 1966) provided a great stimulus to conoidean taxonomy, and is used, with modifications, by almost all authors concerned with Turridae. Powell recognized nine subfamilies which were based primarily on shell characters, although radular and opercular

Table 5. Comparison of character states between Pervicaciinae and Terebrinae.

Character	Pervicaciinae	Terebrinae
Shell shape	Multiwhorled	Multiwhorled
Radular teeth	Solid sickle-shaped	If present, usually hollow enrolled marginals
Odontophore	Present	Present in some <i>Hastula</i> species
Radular caecum	Absent	Present in hollow-toothed forms
Venom gland	Absent	Present in all with radula & proboscis absent in others
Proboscis	Absent	Present in all radulate forms
Salivary glands	Present	Present in many species
Accessory salivary glands	Absent	Present in some species
Rhynchodeal introvert	Present	Present
Rhynchodeal septum	Present in some	Present in some
Accessory proboscis structure	Present in some	Present in some
Eyes	Absent in all?	Present
Operculum	Present	Present

features were also used. Powell believed that the hypodermic toxoglossate dentition could develop independently in different lineages and, more importantly, that the appearance of toxoglossate radula was not a significant reason for separating groups at the subfamilial level. As a result, he classified some taxa having quite different radular types (including both solid and hollow marginal teeth) within a single subfamily.

Morrison (1966) followed Thiele in recognizing a fundamental difference between groups with solid (= nontoxoglossate) and hollow (= toxoglossate) marginal teeth. He suggested a separation at the family level using the families Turridae (with subfamilies Drilliinae, Clavatulinae and 'Lophiotominae or Crassispirinae'), Mangeliidae and 'Pseudomelatominiae'.

The subfamily classification of Powell was considerably revised by McLean (1971), who adhered strictly to the principle of grouping together genera with the same type of radula. He also added six subfamilies to Powell's classification; three of these being described as new (Clathurellinae H. & A. Adams, erroneously). Several subfamilies were recognised (or retained after Powell) on shell characters, but which share the same radular type, and some of these seem to be rather poorly documented. However, McLean's classification which includes 15 subfamilies is at present the most detailed and well developed.

In a continuing series of papers concerning South African Turridae, Kilburn (1983, 1985, 1986, 1988), adopted a pragmatic approach (Kilburn, 1983 p.550 '... any practical subdivision is better than none ...'), and revised to some extent the composition of subfamilies which he studied. He also synonymized the Diptychomitridae (= Mitrolumninae = Mitromorphinae) with the Borsoniinae.

Bogdanov (1986, 1987, 1990) described a new subfamily Oenopotinae separating the operculate *Oenopota* and its relatives from the Mangeliinae. Additionally, the subfamily Taraninae was recently re-instated (Kantor & Sysoev, 1989).

Some nomenclatural changes in the names and authorships of several subfamilies were made by Cernohorsky (1972, 1985, 1987), and Ponder and Waren (1988).

A different viewpoint was taken by Bouchet and Warén (1980) in their study of North Atlantic deep-sea Turridae. They avoided the use of any subfamilial divisions, considering the present classification of Turridae to be artificial and based mainly on (p. 5) '... more or less randomly selected shell characters'.

At present there is no completely agreed classification of Turridae, nor is there any agreement on which are the taxonomically important characters. The existing variants of turrid classification are based almost exclusively on shell, radular and opercular features.

The Terebridae have similarly been classified mainly on shell characters. H. & A. Adams (1853) and Cossmann (1896) divided the Terebridae into two subfamilies, including the Pusionellinae as the second subfamily. *Pusionella* is now known to belong to the turrid subfamily Clavatulinae. A separate family, the Pervicaciidae, was proposed by Rudman (1969) for *Pervicacia tristis*. However, Bratcher & Cernohorsky (1987) included *Pervicacia* and similar forms in the Terebridae. Taylor (1990) confirmed the distinctiveness of *Pervicacia*, and showed that many other terebrids should be included in the family Pervicaciidae.

The Conidae have long been considered as a fairly homogeneous group, the main problems have concerned the limits

of the family and whether taxa such as *Cryptoconus*, *Conorbis* and *Genota* should be included. Cossmann (1896) for example, included them in the subfamily Conorbinae within the Conidae, whilst Powell (1966) includes this subfamily in the Turridae.

New classification proposed

As a result of our analysis of foregut characters throughout all the conoidean higher taxa we propose a new classification of the superfamily. This classification represents a rather conservative compromise position. Although in principle the classification should be based upon the results of the phylogenetic analysis, we were constrained by the rather poor resolution obtained with our data set. Moreover, only a rather small subset of conoidean species have been examined in any detail. Information from taxa not included in the cladistic analysis (mainly radular characters) has also been used in constructing the classification. An example of the problem is the family Turridae, which comprises the four subfamilies with wishbone marginal teeth, plus the Zonulispirinae. The cladistic analysis suggests two different clades for these subfamilies. This is certainly possible, but the branches are supported by rather few, and perhaps weak apomorphies. Despite the deficiencies this is the first comprehensive classification of the Conoidea which includes anatomical characters. Below we give descriptions of shell, radula and foregut characters for each of the higher taxa that we recognise. Some of the taxa have only provisional status. For example, the subfamily Clathurellinae has been divided up into five informal groups; it may well be polyphyletic, but we have insufficient evidence to resolve the situation. Similarly, we are uncertain of the status of the Conorbinae and Taraninae.

Summary of proposed classification

- Superfamily Conoidea
 - Family Drilliidae (ICZN pending)
 - Family Terebridae
 - Subfamily Pervicaciinae
 - Terebrinae
 - Family Pseudomelatomidae
 - Family Strictispiridae
 - Family Turridae
 - Subfamily Clavatulinae
 - Crassispirinae
 - Zonulispirinae
 - Cochlespirinae
 - Turrinae
 - Family Conidae
 - Subfamily Clathurellinae
 - Coninae
 - Conorbinae ?
 - Oenopotinae
 - Mangeliinae
 - Daphnellinae
 - Taraninae ?

DIAGNOSES OF HIGHER TAXA

Family **Drilliidae** Morrison, 1966 (ICZN pending)

Shell of small to medium size (usually 15–25 mm, up to 50 mm), claviform (with a more or less high spire, and a relatively short, truncated base). Anterior canal indistinct, short or moderately elongate. Anal sinus on the shoulder, rather deep, often sub-tubular when a parietal tubercle is present. Sculpture usually well developed. Protoconch paucispiral or multispiral, smooth or, sometimes, carinate (from the second whorl or, rarely, from the beginning). Operculum with terminal nucleus.

RADULA. With strong radular membrane, five teeth in each row, with in some species the complete loss of the central tooth and reduction of the laterals. Rachidian tooth small, with a prominent central cusp and, often, smaller lateral denticles. Lateral teeth are typically broad and curved, comb-like, with many small cusps the outermost being smaller. Marginal teeth have a variable morphology from simple and flat, sometimes with a weak accessory limb, to enrolled. In at least one species (*Imaclava unimaculata*), marginal teeth are hollow and enrolled, whilst the radula as a whole is similar to that of other drilliids.

FOREGUT. Proboscis moderately long, with one or two distal sphincters and sometimes a mid-buccal tube sphincter. Buccal mass at base of proboscis, odontophore well-developed, cartilages either separated or fused. Two acinous salivary glands with two ducts. No accessory salivary glands. Venom gland with uniform histology along its length. Retractor muscle of the radular sac passes through the nerve ring and joins the columellar muscle.

REMARKS. The anatomy and radula are known for only a very few species of Drilliidae. This prevents us from introducing any subfamilial classification of this possibly complex family.

Family **Terebridae** Mörch, 1852

Elongate, multiwhorled shells, with small quadrate to triangular apertures. Siphonal canal short. Anal sinus not visible. Shell ornament of low axial ribs and grooves, spiral grooves, a few species with tubercles, shells often smooth and polished. Protoconch of 1.5–5 whorls. Operculum rounded with terminal nucleus. Radula with solid sickle-shaped teeth, hollow harpoon-like teeth or absent. Rhynchodeal introvert present. Accessory proboscis structure and rhynchodeal septum present in some species. Proboscis present or absent. Odontophore present in some species. Radular caecum present in some. Acinous salivary glands present. Accessory salivary glands present in some species. Venom gland present or absent.

Subfamily **Perviciinae** Rudman, 1969

Shells medium to large, elongate, multiwhorled, anterior canal short, ornament low axial ribs, spiral grooves, often with a subsutural groove. Aperture quadrate. Operculum rounded with terminal nucleus.

RADULA. With strong radula ribbon, two rows of sickle-shaped solid marginal teeth.

FOREGUT. Rhynchodeal introvert. Rhynchodeal septum and accessory proboscis structure present in some species. Proboscis absent. Extensible buccal lips present in some species. Odontophore with two cartilages. Two acinous salivary glands and ducts. Venom gland and accessory salivary glands absent.

Subfamily **Terebrinae** Mörch, 1852

Shells medium to large, elongate, multiwhorled. Small quadrate to triangular aperture. Short siphonal canal. Shells often smooth and polished. Shell ornament of low axial and spiral ribs and grooves.

RADULA. Where present, long, hollow marginal teeth with narrow bases, barbed or unbarbed. *Hastula bacillus* has semi-enrolled teeth with a distal solid blade. Many species have no radula.

FOREGUT. Rhynchodeal introvert present. Rhynchodeal septum and accessory proboscis structure present in some species. Proboscis long, medium or absent. Odontophore with cartilages present in some *Hastula* species. Radula caecum present in many radulate species. Acinous salivary glands with two ducts usually present. Accessory salivary glands present in some species. Venom gland present or absent in radula-less species.

Family **Pseudomelatomidae** Morrison, 1966

Shells of medium to large size (35–77 mm), fusiform. Anterior canal moderately elongate. Anal sinus on the shoulder. Protoconch smooth. Operculum with terminal or subcentral nucleus. Egg capsules dome-shaped, with an operculum.

RADULA. With strong radular membrane; three teeth in each radular row. Rachidian is large and rectangular with a large, curved and pointed, central cusp and smaller lateral cusps. Marginal teeth are solid, simple and curved.

FOREGUT. Proboscis very long, no anterior buccal tube sphincter; buccal mass basal or posterior of the proboscis base. Oesophagus elongated between the buccal mass and nerve ring in *Pseudomelatoma*. Odontophore very large with fused cartilages. Acinous salivary glands, paired in *Pseudomelatoma*, but unpaired with a single duct in *Hormospira*. No accessory salivary glands. Venom gland with uniform histology.

Family **Strictispiridae** McLean, 1971

Shell of rather small size (usually 15–20 mm), claviform. Anterior canal short or indistinct. Sculpture well developed. Deep subtubular sinus is situated on the concave shoulder and bordered with well developed parietal callus. Protoconch smooth, multispiral. Operculum with terminal nucleus.

RADULA. With strong radular membrane; 2 teeth in each row, central and lateral teeth absent (latter maybe diaphanously on optical preparations). Marginal teeth solid, awl-shaped, with pointed tips, a broad base and a mid-tooth flange.

FOREGUT. Proboscis short; buccal mass located near the proboscis tip, odontophore very large and muscular with separate cartilages. Acinous salivary glands small and paired, no accessory salivary gland, no venom apparatus.

REMARKS. This small family possesses unique radular teeth and anatomy, but study of further material is necessary.

Family **Turridae** H. & A. Adams, 1853

Radula always with a membrane with either 3 radular teeth in a row (central being small or weak), 4 (central lost, laterals diaphanous) or with only marginals. Marginal teeth usually wishbone type, rarely enrolled and hollow. Odontophore always present. Radular sac not subdivided into short and long arms. Venom gland always present. Salivary glands always acinous. Accessory salivary gland either present or absent. Operculum present.

Subfamily **Clavatulinæ** Gray, 1853

Shell medium-sized (usually 15–30 mm, maximum 60 mm), variable in form. Anterior canal moderately long, sometimes short or truncated. Whorls usually adpressed below the suture. Anal sinus located on the shoulder slope, rather deep but sometimes indistinct. Protoconch smooth, of 1.5–3 whorls. Axial sculpture predominates or the sculpture is subobsolete and the shell surface is glossy. Operculum ovate, with medio-lateral nucleus. Egg capsules lens-shaped, vertically orientated, without an operculum. Capsules attached to the substratum by a stalk on the edge.

RADULA. Strong radular membrane with 3 to 2 teeth in each row. Central tooth with large, very thin, inconspicuous, basal plate and centrally thickened area with a single cusp. Central tooth sometimes absent (*Toxiclionella* s.s.). Lateral teeth absent. Marginal teeth usually robust wishbone type; hollow harpoon-shaped and barbed in *Toxiclionella*.

FOREGUT. Epithelium of posterior rhynchocoel not glandular and continuous with proboscis. Moderately long proboscis with 1 or 2 anterior buccal tube sphincters. Protrusive lips of the buccal tube may be present (*Turricula*). Buccal mass distal except *Clavatula diadema* in which it is basal but lies within the proboscis. Odontophore medium to small in size, cartilages unfused (except in *Toxiclionella*). Salivary glands acinous, usually paired. Single salivary duct in *Clavatula caerulea*. Single accessory salivary gland in *Toxiclionella*. Anterior venom gland ciliated. Oesophagus elongated between buccal mass and nerve ring.

REMARKS. Some species in this subfamily possess hollow 'toxoglossate' radular teeth associated with strong radular membrane, sometimes, with central teeth. The anatomy and conchological characters of 'toxoglossate' clavatulines are, however, quite similar to those of 'nontoxoglossate' ones. Thus at present we do not consider the appearance of hollow teeth in *Toxiclionella* to be a taxonomic character of subfamilial importance and therefore follow Kilburn (1986) in classifying *Toxiclionella* with other clavatulines.

The genus *Turricula* Schumacher, 1817 appears very similar to clavatulines in both radular characters and anatomy (the distal buccal mass, ciliated anterior venom gland,

elongated oesophagus between the buccal mass and nerve ring). Moreover, it is also similar to clavatulines in shell characters and in its operculum with mediolateral nucleus. On the other hand, *Turricula* differs in both shell and anatomical characters from those of other 'Turriculinae'. Thus we transfer this genus, as well as *Makiyamaia* which has similar characters, to the subfamily Clavatulinæ.

Subfamily **Crassispirinae** Morrison, 1966

Shell of medium to small size (usually 10–20 mm, sometimes up to 70 mm), claviform to fusiform. Anterior canal usually short. Anal sinus on the whorl shoulder, parietal callus above the sinus often well developed. Spiral and axial sculpture often strong. Protoconch usually paucispiral, initially smooth, later sometimes with axial (rarely spiral) folds. Operculum with terminal nucleus.

RADULA. Strong radular membrane and 4, 3 or 2 teeth in each row. Central tooth when present (*Turridrupa*) is thin, quadrate and unicusate, lateral teeth usually absent but weak and vestigial in *Crassispira* and *Crassiclava*. Marginal teeth, robust wishbone type or long flat teeth with a slender accessory limb. *Ptychobela* has hollow teeth formed from two components.

FOREGUT. Proboscis moderately long with two anterior buccal tube sphincters. Epithelium of posterior rhynchocoel continuous with proboscis (*Funa latisinuata*). Buccal mass situated at the proboscis base in its contracted state. Odontophore medium to small, with fused cartilages. Salivary glands acinous, fused, ducts paired. Anterior venom gland ciliated in some species. Oesophagus elongated behind buccal mass in some species.

REMARKS. This most large and diverse subfamily of Turridae is defined chiefly on shell and radular characters (i.e. rather small claviform shells with wishbone radular teeth). Data on the anatomy of its representatives are still insufficient to decide certainly whether the subfamily is of mono- or polyphyletic origin.

Subfamily **Cochlespirinae** Powell, 1942

Shell of medium to large size (usually 20–40 mm, up to 100 mm), narrow to broadly fusiform or pagodiform. Anterior canal moderately elongate, rarely short or very long. Sculpture variously developed, often with smooth shoulder, and usually with rather short axial ribs below the shoulder, and spiral riblets. Anal sinus usually deep, situated on the shoulder (sometimes on its lower part). Protoconch usually multi-spiral, smooth or, sometimes, initially smooth and carinated or spirally or axially lirated on subsequent whorls. Operculum with terminal nucleus.

RADULA. Strong radular membrane, with three, four? (see discussion of radula p. 135) or two teeth in each row. Central tooth weak, unicuspid or absent. Marginal teeth of robust wishbone type.

FOREGUT. Proboscis usually long, with one or two anterior buccal tube sphincters. Buccal mass basal, muscular buccal lips may be present or absent. Odontophore small, cartilages 4, 2 or absent, fused or separate. Salivary glands acinous,

paired or fused. Single accessory salivary gland in *Aforia*.

REMARKS. Since the type-genus of the subfamily Turriculinae, *Turricula* Schumacher, 1817, is transferred to the Clavatulinae (see above), the next available name for this group is Cochlespirinae Powell, 1942.

Subfamily Zonulispirinae McLean, 1971

Shells rather small (15–25 mm), claviform. Anterior canal usually short, sometimes moderately long. Predominantly spiral sculpture, well developed. Protoconch multispiral, initially with smooth whorls, then with oblique axial riblets. Anal sinus on the shoulder, often sub-tubular, with well developed parietal callus. Operculum with terminal nucleus.

RADULA. With strong membrane and marginal teeth in each row. Teeth semi-enrolled, to rolled, hollow teeth with narrow base. Tips may be barbed or unbarbed.

FOREGUT. Proboscis long, with a single distal buccal tube sphincter. Buccal mass distal. Odontophore small with two unfused cartilages. Buccal lips present. Salivary glands fused. Anterior of venom gland ciliated. Oesophagus elongated between the buccal mass and nerve ring.

Subfamily Turrinae H. & A. Adams, 1853

Shell usually of medium to large size (up to 110 mm), fusiform. Anterior canal elongated and narrow, rarely truncated. Anal sinus on the whorl periphery. Axial sculpture weak or absent. Protoconch smooth in its initial part, subsequent whorls axially costate; paucispiral protoconchs smooth. Operculum with terminal nucleus. Egg capsules dome-shaped, operculate.

RADULA. Strong radular membrane, 2–3 teeth in each row. Central tooth either well-developed, small or absent, quadrate to rectangular with a strong central cusp. Lateral teeth absent. Marginal teeth of robust wishbone type.

FOREGUT. Proboscis moderately long, rhynchostomal sphincter posterior, a single distal buccal tube sphincter, protrusive lips of buccal tube present. Buccal mass basal. Odontophore small with fused cartilages. Salivary glands paired. No accessory salivary glands. Anterior part of venom gland ciliated.

Family Conidae Fleming, 1822

Radula consisting of hollow marginal teeth only. Radular membrane absent. Radular diverticulum divided into short and long arms. Odontophore absent. Radula and venom gland may be absent. Salivary glands acinous or tubular. Accessory salivary gland either present or absent. Operculum either present or absent.

Subfamily Clathurellinae H. & A. Adams, 1858

Shell small to rather large, fusiform to biconic. Anterior canal short or indistinct to moderately elongate. Sculpture predominantly spiral in most genera. Anal sinus deep to very

shallow, on the shoulder slope or on the periphery. Columella with or without pleats. Protoconch usually paucispiral, smooth, sometimes carinate or weakly spirally ribbed, rarely axially costate on its last whorl. Operculum with terminal nucleus present, vestigial or absent.

RADULA. Awl- or harpoon-shaped marginal teeth, without (very rarely with) solid base, tooth cavity opens terminally at the proximal end in vast majority of species.

FOREGUT. Proboscis short to long, 1 or 2 anterior buccal tube sphincters, buccal mass basal. Short buccal lips in *Tropidoturris*. Odontophore absent, radular caecum present — divided by septum in *Bathytoma* (*Micantapex*). Salivary glands tubular in *Borsonia*, acinous in others, paired, single or absent. Single accessory salivary gland present in some species. Venom gland with uniform histology. No elongation of oesophagus.

REMARKS. This subfamily comprises species classified by other workers in the subfamilies Borsoninae and Clathurellinae. Being very variable in both anatomical and shell characters, the subfamily may be of polyphyletic origin. More species need to be studied anatomically before any satisfactory classification can be attempted. The subfamily is defined mainly by the character of the radular teeth. Several groups of genera can be isolated within Clathurellinae according to shell characters.

'Clathurellid' group is characterized by medium-sized shells (usually 10–25, up to 40 mm), with a moderately elongate siphonal canal, and a well developed, often cancellate sculpture. Columella without pleats, but both inner and outer lips may be denticulated; anal sinus deep located on the shoulder. Protoconch usually multispiral, last whorls with a pronounced medial carination and, sometimes, weak axial lamellae on the lower half. A distinctive feature of this group is densely granulated shell surface of most genera (except of one subgenus of *Glyphostoma* and, probably, *Nannodiella*). Operculum absent. Radular teeth long and slender, slightly curved, without a solid base.

'Bathytomid' group. Shell of medium to rather large size (usually 20–30, up to 70 mm), more or less biconic. Sculpture usually well developed, entirely spiral, ribs often gemmulated by growth lines; typically there is a peripheral tuberculated flange. Anal sinus rather deep, located on the whorl periphery. Columellar pleats strong to obsolete. Protoconch of 1.5–3 whorls, smooth or minutely papillated. Operculum with terminal nucleus. Radular teeth either long, with more or less terminal opening, or short, with large cylindrical solid base and lateral opening.

'Borsoniid' group. Shell of rather small to medium size (usually 15–25, up to 62 mm), fusiform. Anterior canal moderately elongate, sometimes long. Both spiral and axial sculpture may be present. Columellar pleats weak or absent. Anal sinus on the shoulder slope. Protoconch of 1–2 smooth whorls. Operculum fully developed, small or absent. Radular teeth long, without solid base, open terminally, or, rarely, short, with large cylindrical base, open laterally. Egg capsules dome-shaped, with an operculum.

'Mitromorphid' group. Shell small (usually 4–8, up to 17 mm), biconic and 'mitriform'. Anterior canal very short or indistinct. Aperture narrow, columella with or without teeth, outer lip usually denticulated, anal sinus shallow and sub-tubular. Sculpture predominantly or entirely spiral. Protoconch of 1.5–2 smooth whorls. Operculum absent. Radular teeth

rather short, of 'candle flame' shape, open terminally.

'Tomopleurid' group. Shell rather small to medium sized (6–7 to 37 mm), claviform, with flattened whorls. Anterior canal short. Anal sinus on the shoulder or just below it, moderately deep. Columellar pleats absent. Sculpture entirely spiral (except often raised growth lines), consisting of well developed ribs or heavy keels. Protoconch pauci- or multispiral. In the former case it is smooth or with minute spiral striae or papillae, sometimes carinated; in the latter case first 1–3 whorls with the same sculpture, later ones with axial ribs and, sometimes, minute spiral striae. Operculum with terminal or eccentric nucleus, sometimes absent. Radular teeth short or long and slender, without solid base, open terminally.

Subfamily **Conorbinae** De Gregorio, 1890

Shell of medium size (up to 40 mm), biconic. Anterior canal short, aperture long and narrow. Sculpture entirely spiral except the growth lines. Anal sinus on the shoulder or almost sutural, relatively deep. Protoconch multispiral, smooth or spirally striated on later whorls. Operculum present or, absent in *Conorbis*.

RADULA. Hollow, marginal teeth with barbed tips and narrow bases (*Conorbis*, Thiele, 192 fig 460; *Benthofascis*, Powell, 1966, fig. 125).

FOREGUT. These observations are based on *Benthofascis*. Rhynchostomal sphincter posteriorly situated. Proboscis moderately long, not folded telescopically as in *Conus*. Distal sphincter of buccal tube absent, intermediate sphincter present. Middle part of buccal tube lined with glandular epithelium. Single acinous salivary gland with two ducts. Single accessory salivary gland. Venom gland with uniform histology, muscular bulb with two muscular layers. No snout gland.

REMARKS. The status of this subfamily is uncertain due to lack of any anatomical information on *Conorbis*. We have excluded *Genota* on the basis of shell morphology and the absence of the operculum.

Subfamily **Coninae** Fleming, 1822

Shell of medium to large size (usually 30–50 mm, up to more than 120 mm), biconic to conic. The inner shell walls are partially resorbed. Anterior canal short, aperture usually narrow, parallel-sided. Sculpture entirely spiral, usually weak or obsolete, sometimes tubercles on the shoulder. Anal sinus on the upper shoulder or almost sutural, shallow to relatively deep, occupying a rather narrow zone. Protoconch multispiral, smooth or spirally striated. Operculum small, with terminal nucleus, rarely absent. Egg capsules, bilaterally flattened, vasiform, arranged in clusters.

RADULA. Radular teeth harpoon-shaped, barbed or unbarbed on the tips, without solid base, usually open terminally (rarely laterally) at the base.

FOREGUT. Proboscis moderately short and folded in contracted state. Rhynchostome lacks definite sphincter and rhynchodaeum can be greatly expanded to form a rostrum in fish-feeding species. Radial muscles lie in rhynchodeal wall.

Snout gland present in many species. Distal buccal tube sphincter absent, intermediate sphincter present. Middle part of buccal tube is lined with glandular epithelium. Buccal mass basal. Single acinous salivary gland with one or two ducts. Single accessory salivary gland. Venom gland of uniform histology, muscular bulb often with many muscular layers.

Subfamily **Oenopotinae** Bogdanov, 1987

Shell of small to medium size (usually 10–15, up to 30 mm), oval to fusiform. Anterior canal rather short. Both spiral and axial sculpture well developed. Anal sinus on the shoulder, shallow, and often indistinct. Protoconch paucispiral, predominantly (sometimes entirely) spirally sculptured. Operculum with terminal nucleus present, vestigial, or rarely absent. Egg capsules dome-shaped, with an operculum.

RADULA. Radular teeth with rounded or cylindrical solid base and hollow shaft, sometimes with barbed tip; rarely teeth vestigial; tooth cavity opens laterally between the shaft and the base.

FOREGUT. Proboscis either long, or short and folded in contracted state. Distal sphincter present or absent. Buccal lips large, may be inverted into the buccal cavity. Buccal mass basal. Salivary glands paired, acinous, although shown as tubular (probably erroneously) in *Oenopota levidensis* Shimek (1975). Venom gland of uniform histology. Muscular bulb with a thin outer muscular layer.

REMARKS. Species of this group were previously treated as Mangeliinae, but were isolated as a subfamily primarily on the basis of the presence of an operculum and a spirally sculptured protoconch (Bogdanov, 1987, 1990). None of these features are presently considered as being of subfamilial importance. However, one more character was revealed in our study, the structure of the salivary glands, which distinguished Oenopotinae from the Mangeliinae. We provisionally retain the subfamilial rank of Oenopotinae until the systematic importance of this character becomes certain.

Subfamily **Mangeliinae** Fischer, 1884

Shell small (usually 5–12 mm, up to 20 mm), ovate to fusiform. Anterior canal rather short. Both spiral and axial sculpture well developed. Anal sinus on the shoulder, shallow to rather deep, sometimes subtubular. Outer lip usually with terminal varix, sometimes denticulate. Protoconch smooth or variously sculptured. Operculum absent. Egg capsules dome-shaped, with an operculum.

RADULA. Radular teeth hollow with a solid base, sometimes with a semi-enrolled shaft; tooth canal opens laterally.

FOREGUT. Proboscis moderately long, with a single or no distal sphincter, intermediate and posterior sphincters sometimes present. Buccal tube introvert ('valvule') present. Distal lips of buccal tube can be inverted. Buccal lips large and can be introverted into the buccal cavity. Buccal mass basal. Salivary glands paired and tubular, accessory salivary glands absent. Venom gland of uniform histology; muscular bulb usually with a thin outer muscle layer.

Subfamily *Daphnellinae* Deshayes, 1863

Small to moderately large shells (usually 5–15 mm, deep-sea species larger, up to 95 mm). Anal sinus sutural, shaped as a reversed-L, or on the upper shoulder and varying in depth. Sculpture variable, usually cancellate or with predominant spirals, and often with a smooth shoulder. Protoconch usually multispiral, rarely paucispiral, typically diagonally cancellated, although some genera have spiral or axial ribbing. Operculum absent. Egg capsules dome-shaped operculate.

RADULA. Radular teeth with large solid base and barbed or unbarbed tips, tooth cavity opens laterally at the base. Radula absent in some species.

FOREGUT. Rhynchodeal introvert present in many species. Rhynchodeal septum present in some species. Proboscis usually short, often absent. Buccal mass basal. Radula apparatus absent in many species, vestigial in *Gymnobela emertoni*. Radial muscles present in the rhynchodeal wall in radula- and proboscis-less species. Buccal lips well developed, can be inverted into the buccal cavity. Salivary glands paired tubular or absent. Accessory salivary glands absent. Venom apparatus absent in many species. In *Daphnella reeveana* the anterior part of venom gland is ciliated. Muscular bulb can be single layered.

REMARKS. Although *Thatcheria* is sometimes classified in a separate subfamily Thatcherinae, we failed to find any anatomical or shell characters which would justify separation from the Daphnellinae.

Subfamily *Taraninae* Casey, 1904

Shell very small (up to 6 mm), ovate-fusiform. Anterior canal rather short. Sculpture well developed. Anal sinus very broad and shallow, situated on the shoulder or immediately below it. Protoconch paucispiral, finely spirally striated, or with spirally aligned granules. Operculum and radula absent.

FOREGUT. Rhynchostomal sphincter absent, no radial muscles in rhynchodeal wall. Proboscis absent. Buccal mass undefined. Salivary glands absent. Venom apparatus absent.

REMARKS. This monotypic radula-less subfamily was reinstated (Kantor & Sysoev, 1989) because it differs in shell characters from any other turrids lacking a radula. However, the very simplified morphology makes the evaluation of the status of the subfamily difficult. For the present we conserve the subfamily, but are unsure of its status.

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APPENDIX 1

Features of the shell

Shell characters are still important for the systematics of Conoidea, and thus should be included in the analysis. However, there is probably no shell character which is diagnostic of any single group. Moreover, there has been no analysis of the adaptive or evolutionary significance of these shell features. Nevertheless, a few shell characters appear to be useful for the separation of clades.

Shell shape

This character which is concerned with overall shell shape is the most subjective. We recognise five basic shell shapes: 1, fusiform shell; 2, cone-shaped shell; 3, turreted shell; 4, terebriform shell; 5, a large group of 'intermediate' states, 'biconic-fusiform', 'ovate-biconical', 'ovate-fusiform', 'claviform', etc. characterized by rounded outlines of the shell, which is more or less oval in its general profile.

Number of protoconch whorls

Two types of protoconch can be recognised; the paucispiral and multispiral. These types of the protoconch were introduced into turrid systematics by Powell (1942, 1966) and they are widely used in taxonomy. Generally, this subdivision coincides with that between planktotrophic and non-planktotrophic modes of larval development, although there are many exceptions to the rule among turrids (Bouchet, 1990). The character is considered as being of little phylogenetic importance (Bouchet, 1990), but a predominance of a single type of the protoconch can be noted in some taxa. For instance, most Daphnellinae and Conidae have multispiral protoconchs, whilst the paucispiral type is a typical of the Oenopotinae (Bogdanov, 1990). Protoconchs with 1–2 whorls are here considered as paucispiral, and these with two or more whorls as multispiral (Bouchet, 1990).

Sculpture of the protoconch

The pattern of protoconch sculpture has been widely used in conoidean taxonomy since Powell (1942, 1966). Turrids have a very wide variety of protoconch sculpture and at present, we are unable to classify them into clearly defined types. Thus we recognize only two major states of the character; firstly protoconchs lacking or with only weakly defined sculpture and secondly, protoconchs with well developed sculpture. Some higher taxa may be characterized by the presence or absence of protoconch sculpture. For example, the closely-related *Turricula* and *Clavatula* usually possess a smooth protoconch, whilst in the Turrinae it is usually axially costate. The only type of the protoconch sculpture characteristic of a single subfamily is the 'diagonally cancellated' form found

among species of Daphnellinae, although this is not present in all species.

Length of siphonal canal

To define groups of shells with different lengths of the anterior siphonal canal we used parameter Rsl (relative siphonal length) of Harasewych (1981). As a result, we recognise three states of the character; a long siphonal canal (Rsl more than 0.39; up to 0.48 in the species studied), moderate canal (Rsl 0.21 to 0.34), short canal (Rsl less than 0.20) or not differentiated from the apertural canal.

Position of the anal sinus

The anal (labial) sinus is a characteristic feature of Turridae and its position on the shell whorls is widely used for characterizing species and higher taxa (Powell, 1942, 1966; McLean, 1971). We follow Powell (1966) in recognizing 4 types of sinus position; sutural (the deepest point of the sinus is situated near the suture), subsutural (on the whorl shoulder), peripheral, and poorly pronounced (or very slight). Most turrids have a subsutural sinus; a peripheral sinus is characteristic for all Turrinae and some Clathurellinae (*Bathytoma* and related genera); a sutural sinus is common among the Daphnellinae. A weak, almost imperceptible sinus occurs occasionally in many subfamilies. It should be emphasized that sinus types are recognized by growth lines, since the form of sinus at the outer lip of a mature shell may not be the same as that of the immature gastropod.

Operculum

The presence of an operculum is obviously the primitive state of the character. All 'lower' conoideans have a well developed operculum. Among 'higher' conoideans, the operculum is absent in almost all Daphnellinae and Mangeliinae, but retained in the Oenopotinae and Conidae. In Clathurellinae (incorporating Borsoniinae), the operculum may be present, vestigial or absent, even in apparently closely-related genera (McLean, 1971).

Position of opercular nucleus

The opercular nucleus is usually situated in a terminal position at the tip of the operculum, but in the Clavatulinae and *Turricula* it is located medio-laterally.

Presence of apertural armament

The aperture of conoidean shells may be without ornament on the outer lip or columella, or they may bear weak to strong denticles, plications and folds. Armed apertures are found in the subfamilies Mangeliinae, Clathurellinae and Daphnellinae, and mostly amongst tropical shallow-water species.

Number of teleoconch shell whorls

We recognize three types of shells by this character. 1. shells with a small number of whorls (4 and less); 2. with an intermediate number of whorls (5 to 8); 3. with many whorls (9 and more)

Presence of well developed subsutural ramp

A subsutural ramp, (a morphologically distinct, often flattened part of the whorl profile immediately below the suture) may be either absent, or pronounced, in many subfamilies of Turridae. Usually, this character is clearly shown by a change in both spiral and axial sculpture in this region of the whorl.

APPENDIX 2

Genus-group taxa of recent Turridae S.L. (Compiled by A.V. Sysoev)

The list presented below is of Recent taxa of the genus-group of Turridae s.l. distributed in respect to the classification adopted in the present paper. Since all the data concerning genera described before 1966 were given in Powell's (1966) monograph, type-species and bibliographic citations are included only for genera and subgenera described after 1966. Synonymy is also given only when it differs from that adopted by Powell.

The classification used is to a great extent conservative; we avoid the description of new taxa and radical changes in the existing classification. As a result, some genera are of 'unclear' taxonomic position and cannot be assigned, despite anatomical information, to any existing subfamily (*Toxichlespira*, for example). Some other genera (such as *Genota*) are only provisionally included into a certain subfamily.

There are 337 valid Recent genera and subgenera.

Family DRILLIIDAE Morrison, 1966. ICZN pending

Agladrillia Woodring, 1928

Eumetadrillia Woodring, 1928

Bellaspira Conrad, 1868

Calliclava McLean, 1971

Veliger 14(1): 117

Cymatosyrinx palmeri Dall, 1919

Cerodrillia Bartsch & Rehder, 1939

Lissodrillia Bartsch & Rehder, 1939

Viridrillia Bartsch, 1943

Clavus Montfort, 1810

Plagiotropha Melvill, 1927

Cymatosyrinx Dall, 1889

Drillia Gray, 1838

Clathrodrillia Dall, 1918

Elaeocyma Dall, 1918

Globidrillia Woodring, 1928

Horaiclavus Oyama, 1954

Anguloclavus Shuto, 1983

Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 9-10

Mangilia multicostata Schepman, 1913

Cytharoclavus Kuroda & Oyama in Kuroda, Habe & Oyama, 1971

The sea shells of Sagami Bay: 213

Pleurotoma (Mangilia) filicineta Smith, 1882

Imaclava Bartsch, 1944

Iredalea Oliver, 1915

Kylix Dall, 1919

Leptadrillia Woodring, 1928

- Neodrillia* Bartsch, 1943
- Orrmaesia* Kilburn, 1988
Ann. Natal Mus. 29(1): 201–202
Orrmaesia dorsicosta Kilburn, 1988
- Splendrillia* Hedley, 1922
Hauturua Powell, 1942
- Spirotropis* G.O.Sars, 1878
- Syntomodrillia* Woodring, 1928
- Tylotiella* Habe, 1958
- ?*Acinodrillia* Kilburn, 1988
Ann. Natal Mus. 29(1): 223
Acinodrillia viscum Kilburn, 1988 (s.d. Kilburn, 1988,
Ann. Natal Mus. 29(2): 557)
- ?*Douglassia* Bartsch, 1934
- ?*Fenimorea* Bartsch, 1934
- ?*Paracuneus* Laseron, 1954
- Family PSEUDOMELATOMIDAE Morrison, 1966
- Hormospira* Berry, 1958
Pseudomelatoma Dall, 1918
(= *Laevitectum* Dall, 1919)
- Tiariturrus* Berry, 1958
- Family STRICTISPIRINAE McLean, 1971
- Cleospira* McLean, 1971
Veliger 14(1): 125
Monilispira ochsneri Hertlein & Strong, 1949
- Strictispira* McLean, 1971
Veliger 14(1): 125
Crassispira ericana Hertlein & Strong, 1951
- Family TURRIDAE H. & A. Adams, 1853
- Subfamily CLAVATULINAE Gray, 1853
- Benthoclionella* Kilburn, 1974
Ann. Natal Mus. 22(1): 214
Benthoclionella jenneri Kilburn, 1974
- Clavatula* Lamarck, 1801
- Clionella* Gray, 1847
- Makiyamaia* Kuroda in MacNeil, 1960
- Perrona* Schumacher, 1817
- Pusionella* Gray, 1847
- Scaevatula* Gofas, 1989
Arch. Molluskenk. 120(1/3): 16
Scaevatula pelisserpentis Gofas, 1989
- Toxiclionella* Powell, 1966
Caliendrula Kilburn, 1985
Ann. Natal Mus. 26(2): 442–443
Latiaxis? elstoni Barnard, 1962
- Turricula* Schumacher, 1817
- ?*Makiyamaia* Kuroda in MacNeil, 1960
- Subfamily CRASSISPIRINAE Morrison, 1966
- Aotedrillia* Powell, 1942
- Austrodrillia* Hedley, 1918
Regidrillia Powell, 1942
- Belalora* Powell, 1951
- Buchema* Corea, 1934
- Calcatodrillia* Kilburn, 1988
Ann. Natal Mus. 29(1): 290–291
Calcatodrillia chamaeleon Kilburn, 1988
- Carinodrillia* Dall, 1919
- Carinapex* Dall, 1924
- Ceritoturris* Dall, 1924
- Conorbela* Powell, 1951
- Coticosta* Laseron, 1954
- Crassiclava* McLean, 1971
Veliger 14(1): 121
Pleurotoma turricula Sowerby, 1834
- Crassispira* Swainson, 1840
Burchia Bartsch, 1944
Crassispirella Bartsch & Rehder, 1939
Dallspira Bartsch, 1950
Gibbaspira McLean, 1971
Veliger 14(1): 122
Pleurotoma rudis Sowerby, 1834
Glossispira McLean, 1971
Veliger 14(1): 121
Pleurotoma harfordiana Reeve, 1843
Monilispira Bartsch & Rehder, 1939
Striospira Bartsch, 1950
(= *Adanaclava* Bartsch, 1950)
- Doxospira* McLean, 1971
Veliger 14(1): 124
Doxospira hertleini Shasky, 1971
- Epideira* Hedley, 1918
(= *Epidirona* Iredale, 1931)
- Funa* Kilburn, 1988
Ann. Natal Mus. 29(1): 267–268
Drillia laterculoides Barnard, 1958
- Haedropleura* Bucquoy, Dautzenberg & Dollfus, 1883
- Hindsiclava* Hertlein & Strong, 1955
(= *Turrigemma* Berry, 1958)
- Inodrillia* Bartsch, 1943
- Inquisitor* Hedley, 1918
- Kurilohadalia* Sysoev & Kantor, 1986
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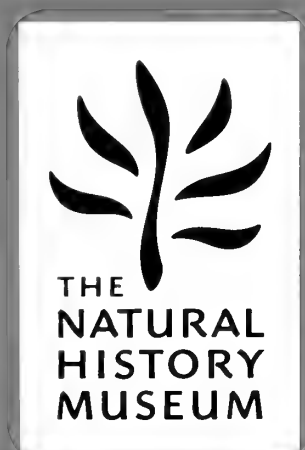
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A new subfamily and genus in Achatinidae (Pulmonata: Sigmurethra)

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SYNOPSIS. In the Achatinidae, characteristics of the internal anatomy, particularly those in the reproductive tract, are continuing to show greater dependability in determining phylogenetic affinities than those in the shell, radula or jaw. In 1934, J.C. Bequaert reached the conclusion in the course of his revising the African land snail family Achatinidae, 'that several of the East African *Achatinae* are not separable from the West Africa *Callistoplepae*, at any rate as far as shell characters go'. The present 5-year study of over 500 shell specimens and 50 soft anatomies, involving 11 genus-group and 57 species-group nomina, demonstrates that the 4 anatomically distinct West African species, to which Bequaert referred, are the most primitive in the family. Accordingly, they have been placed in a separate subfamily. Anatomically the 5 contrastingly different East African species were found to be a distinct genus, plesiomorphic to subgenus *Achatina* (*sensu* Bequaert, 1950). Their phylogenetic relationships show a strong correlation with the distributional evidence in 60 recorded localities, which delineates (1) a short north central axis, (2) a central to eastern Africa axis, and (3) a strong north-south axis extending from eastern Africa into southern Africa. This evidence supports the emerging pattern of terrestrial gastropod distribution in Africa. The present project forms the foundation for a revision of the family, currently in progress.

INTRODUCTION

Fifty-seven species-group nomina associated with the achatinid genus *Callistoplepa* have provided the basis for the present 5-year project. The examination of over 500 shell specimens and 50 soft anatomies has revealed the fact that four West African anatomically distinct but related Lower Guinea species, in two genera, constitute a separate, primitive subfamily of the Achatinidae. Anatomical and conchological studies place the five other valid species in a new genus that is distributed in Central, Eastern and Southern Africa.

Taxonomy in the Achatinidae is based both on the shell and on the soft anatomy, particularly that of the basal reproductive tract. The shell is a permanent record that reflects ontogenetically the influence of the environment, whereas the soft anatomy reflects phylogenetically the influence of evolution. The latter, in the short term, is relatively free of substantive changes, being limited to temporary variations that reflect nutritional, developmental or reproductive influence. For example, both immature and seriously malnourished mature specimens have misleadingly attenuated, thin reproductive tracts with greatly limited musculature; but the malnourished specimen can be readily distinguished because it has a much larger reproductive tract

with the rich coloration of the mature specimen. Under suitable conditions, both types of individuals are able to assume the basic genital proportions that are typical of the species. In the long term, the shell reflects and responds to the pressures of selection in a changing or in a new environment. Wholly different molluscan stocks moving into distinct but similar environments may evolve convergently into forms that are so similar that conchologically they cannot reasonably be distinguished or identified without first knowing the locality, e.g. *Achatina* (*Lissachatina*) *craveni* Smith, 1881 and *A. (Achatina) tavaresiana* Morelet, 1866 (Mead, 1992). Although in the long term, the soft anatomy undergoes changes, it revealingly does so within a more restricted, basic, generalized pattern obviously characteristic of the larger group of which it is a related part. At this stage of investigations, these larger groups seem to be taking shape within genera and subgenera (*sensu* Bequaert, 1950).

All these factors have so entered into the present project that nine species, once thought to be congeners on the basis of the great similarity in their familial unique shell characters, are now separated into two subfamilies. The shells are remarkably similar, but the soft anatomies convincingly tell a different story. In essence, in the Achatinidae the soft anatomy reveals dependable, differentiating taxonomic criteria at the species level and above; the shell usually reveals supporting taxonomic criteria at the species level and often convincing criteria at the subspecies level. A more clear concept of subspecies is beginning to emerge in this family: Essentially consistent, usually minor shell differences in the members of an allopatric population that have features in their soft anatomy indistinguishable from those of the nominate subspecies. This is precisely why the erstwhile enigmatic *Leptocala petitii* is shown in the text to be a distinct species rather than a subspecies or a synonym of the conchologically very slightly different *L. mollicella*.

The shells of the nine species in this project have been redescribed in the light of larger series of specimens and more detailed examinations of shell characters than in previous studies. In many full grown specimens, weathering and environmental abrasion have obscured or removed valuable shell characters, particularly in the upper whorls. The emphasis on a comparative examination of juvenile specimens in the present study, therefore, has been especially informative. In fact, it strongly supports the value of the collecting juvenile specimens, along with the larger specimens, whenever they are available. For the same reasons, determining the number of whorls is always an imprecise measurement and thus is recorded here only to the nearest one-quarter whorl. The length of the last whorl (= body whorl) includes the entire whorl and is measured from the base of the aperture to the point on the suture immediately above where the outer lip attaches at the periphery. All shell measurements are carried to the nearest 0.1 mm. For many decades the basic horizontal and vertical sculpture of the achatinid shell has been referred to as 'deccusate'; this has been changed in the present work to the more accurate term 'cancellate'. From the shell dimensions, two important relationships are drawn: 1) between the greatest shell width and the shell length, and 2) between the length of the last whorl and the shell length. These relationships are expressed in percentages rather than in ratios. This emphasizes the measurement being compared rather than the measurement to which it is being compared; that is, in making comparisons, it is easier to comprehend that the last whorl is 87% of the shell length, than the fact that the length

is 1.15 times the length of the last whorl. Aperture width does not include the callus. The descriptive shell terminology is largely based on Cox (1960).

Diligent searching in 49 museums and personal collections, fortunately brought to light an unexpected fair number of alcohol preserved specimens. The museums with the largest and most varied collections of alcohol preserved achatinid specimens are in Tervuren, Stockholm, Berlin, Bruxelles, Paris, Frankfurt and London. But very valuable specimens have been found in museums where there is relatively limited material. It was through the convictions of Edmond Dart-velle of the Muséum National de l'Afrique Centrale (Tervuren) that the wet collection of the museum is unparalleled in quantity and diversity. Because the available material used in the present project is limited, determined efforts were made, after establishing the basic genital pattern, to conserve the remaining specimens for future investigators.

The relationships of the basal genital system show to greater comparative advantage in ventral view. For this reason, the line drawings are similarly oriented in this perspective, with the male conduit to the left and the female conduit to the right, unless otherwise indicated. The individual structures of the conduits are spread apart to show their configuration and minimize obstruction. The drawings are idealized, where possible through multiple specimens, to eliminate irrelevant and misleading features produced in preservation. The origin of the penial retractor is on the male conduit at a point that marks the division between penis and vas deferens. As the retractor anlage reaches apically during development, it usually inserts somewhere on the columellar muscle system, but may insert on the body wall, diaphragm, transverse myoseptum or other sites in the haemocoel (Mead, 1950). The configuration of the developing viscera may predispose the manner of insertion. The not infrequent bifurcate (Fig. 20) and multifurcate penial retractor insertions support the ontogenetic rather than the functional interpretation of these terms. Within a species, the site of insertion may be consistent or variable. There is a fairly strong tendency in this family for the basal penial retractor to proliferate muscle and apparently connective tissue that variously produce adhesions in the several parts of the male conduit. This in turn changes the relationship of these parts, alters the extroversion process, and the configuration of the resultant intromittent organ. This organ is normally composed seriatim, apex to base, of the penis, pilaster (when present), penis sheath, penial atrium and genital atrium externally, and the basal vas deferens, penial retractor, apical vas deferens and ejaculatory duct internally.

Directions of left and right refer to those of the snail. Apical, in reference to the genital system, means toward the ovotestis, basal toward the genital atrium. The anatomical terminology is essentially that of Mead (1950) (see Abbreviations - Anatomical below).

The discussion of each species is in the following format: shell, soft anatomy (where available), type material, type locality, distribution and, when applicable, remarks. The sources and localities of the alcohol-preserved specimens are reported in the text. A table for each species includes the sources of all shell specimens examined, taxonomically important specimens, illustrated specimens, a size range, their localities, shell dimensions and shell proportions. Illustrations in the literature are cited in the synonymies; the nature of the illustration, where it is other than of the shell, is shown in parentheses. Most localities were found in the

volumes of the U.S. Board of Geographic Names and their locality figures were preferentially used. A list of acronyms of institutions and private collections follows the text. Symbols and abbreviations used in the Tables: Holo = Holotype, L = Length, Lect = Lectotype, LW = Last Whorl, Para = Paratype, PLec = Paralectotype, W = greatest Width, † = dissected, * = see photograph.

Continued research along the lines of Mead (1950, 1978, 1992) and in the present work promises to establish a sound taxonomic and phylogenetic base for the Achatinidae.

METHODS

Examining a great number of variously preserved whole specimens in the present project has once again emphasized the importance of using proper preservation procedures. Ideally, specimens selected for preservation of the soft parts should be put in previously boiled water that has reached ambient temperature. They should drown normally 8–12 hours. Overdrowning will cause the basal genital structures to evert, irreparably distorting the taxonomically valuable features. Underdrowning permits the specimen to withdraw excessively into the shell. Crowding the specimens or using too small a volume of fluid promotes maceration. The adequately drowned specimen usually contracts slightly when placed in the initial 40% alcohol. In a few hours, depending upon the size of the specimen, it should next be placed in a 60% solution, followed by at least one change to 70% alcohol.

Formalin is a powerful, penetrating, irritating fixative. If it is used at a very low percentage for a short period before the specimen is washed thoroughly and transferred to 70% alcohol, it can be quite effective. But in general, its use should be avoided because formalin alters the colour of the shell, makes the shell brittle and chalky, causes the periostracum to crack and peel off upon drying, promotes adhesions between the shell and soft parts, severely hardens the muscular body wall, and precipitates great quantities of albumin and recrystallized calcareous islands in the tissues. As a result, extrication rarely can be accomplished without damage to both shell and soft parts. Further, even with prolonged soaking in a 0.5% trisodium phosphate solution, the muscular body wall remains so hard and tough that, with extreme difficulty it has to be snipped out, piece by small piece, to get to the soft parts, which often are so intensely fixed that they are brittle. Once the soft parts are removed, they usually can be relaxed for limited manipulation only by further soaking in trisodium phosphate and one or more prolonged water baths. Even then, a distressing degree of brittleness remains. The practice of ‘neutralizing’ formalin for the preservation of vertebrate specimens by first dropping live snail specimens in the solution is deplorable.

ABBREVIATIONS – ANATOMICAL

AVD	apical vas deferens
BVD	basal vas deferens
E	egg
EM	eversion muscle bands
FO	free oviduct

GA	genital atrium
OTD	ovotestis duct
P	penis
PA	penial atrium
PIL	pilaster
PR	penial retractor
PS	penis sheath
RCR	right columellar retractor
ROR	right ommatophore retractor
S	spermatheca
SD	spermathecal duct
SO	spermoviduct
SSV	secondary seminal vesicle
T	talon
V	vagina
VA	vaginal atrium
VR	vaginal retentor

Achatinidae

Basal genital conduits simple, without accessory organs. A conspicuous sheath partially, or usually, completely envelops the penis. Spermatophores not formed. The right branch of the columella muscle system regularly remains to the left of the genitalia. Kidney long, two to three times the length of the pericardium; sigmurethrous. Pulmonary vein without major branches. Holopod. Rachidian tooth very slender and apparently nonfunctional, rarely wide. Jaw simple; smooth or usually striated. Shell ovate, elongate-ovate or conic-oblong, rarely columnar; anomphalous or umbilicate; columella truncate or continuous with outer lip, some forms are intermediate. Endemic in continental Africa and its adjacent small coastal islands; four known introduced species elsewhere in the world.

Key to Subfamilies

Vas deferens does not penetrate the penis sheath, but leaves apically with the penial retractor through the sheath aperture. The penial retractor inserts on the right columellar retractor; it is extremely short, entirely or almost entirely covered by the penis sheath; penis contains a large, conspicuous pilaster. Rachidian tooth about as wide as the laterals CALLISTOPLEPINAE

Vas deferens penetrates the penis sheath. Even within a single population, the penial retractor may variously insert on muscle bands, body wall, diaphragm or fascia; it is usually long to very long and entirely or almost entirely free of the penis sheath; penis contains an ill-defined pilaster, no pilaster, or a verge. Rachidian tooth usually much narrower than the laterals ACHATININAE

CALLISTOPLEPINAE – new subfamily

This subfamily contains the most primitive achatinids yet known. Phylogenetically, it is at the base of the Achatinidae, near the Subulinidae. Like that in the Subulinidae, the vas deferens does not penetrate the penial sheath. The more ovate, patterned shell, however, with its larger aperture and limited number of whorls places this taxon in the Achatinidae rather than the Subulinidae. Supportive of this are the long kidney and the pattern of lung venation. The radula is uncharacteristic of either family, but this is of lesser impor-

tance phylogenetically because this structure is well known to be responsive to changing feeding habits within closely related species. The wide, functional rachidian tooth immediately distinguishes the Callistoplepinae from most Achatiniinae (Fig. 58–63). D'Ailly (1896:69) was the first to examine and illustrate the radulae of both species of *Callistoplepa* (see also Pilsbry, 1904:ix,xv; Thiele, 1929:560 and Ortiz & Ortiz, 1959:46). In the present study, the radulae of *C. barriana* (Sowerby, 1890), *C. shuttleworthi* (Pfeiffer, 1856) and *Leptocala mollicella* (Morelet, 1860) were found to follow the same basic form and pattern. Similarly all the jaws are essentially identical – simple, nearly smooth, fulvous, chitinous collariform band that is somewhat wider in the middle and tapering at the sides. There is no suggestion of even generic difference in these structures. Thus, with only two alcohol specimens of *L. petitia* (Jousseaume, 1884) extant, a decision was made to leave their odontophores intact.

All four species in the Callistoplepinae are limited geographically (ca 5° N–5° S) to the tropical Lower Guinea region of West Africa, which at this point appears to be the cradle of the Achatiniidae (Mead, 1992). The high natural luster of their translucent, elongate-ovate shells probably reflects selective advantage in the protractedly wet rainforest. Prior to the present study, the soft anatomy had been examined in one or more species in the eleven achatinine genera except the Guinean genus *Columna* (none so far available) and all except four of the thirteen achatinine subgenera (*sensu* Bequaert, 1950). All that have been examined clearly are anatomically more advanced than the two callistoplepine genera.

The calcareous, thick-shelled eggs are comparatively large for the family and are on a par with those of *Tholachatina*. D'Ailly (1896:68) felt they were somewhat small compared to the size of the snail shell. Thiele (1929:560) echoed this point; but d'Ailly apparently was comparing them with the relatively huge eggs of some *Archachatina* and the subulinids. A reticulate-microtuberculate texture covers the slender, attenuated body. Basally, the mantle is generously covered with variable size, fusing black to gray spots; these show through the thin shell. Apically, the spots are smaller, more regular and concentrated on the shoulder of the whorls. The genital orifice appears to be unusually far posterior; Ortiz & Ortiz (1959) made this observation in *C. shuttleworthi*.

Typical of the known achatinids, the anterior aorta in the Callistoplepinae is found on the dorsal surface of the diaphragm where it abruptly penetrates the diaphragm to pass vertically along the anterior edge of the sagittal myoseptum. Anteriorly, this latter separates the right and left columellar retractors and incompletely places the male and female basal conduits in left and right chambers, respectively. In all four species, the triangular kidney is long, 2–3 times the length of the pericardium, and sigmoidurethrous. The ascending limb of the urethra is closed for its entire length. Venation of the lung is a dense, broad network on the pericardial side of the slender principal vein, whereas on the right of the principal vein there is a relatively narrow band of parallel, limitedly branching veins between it and the ascending limb of the ureter. The second largest vein, about half the caliber of the principal vein, starts as a network in the far left posterior corner of the lung, anastomoses, and joins the principal vein at a right angle 5–7 mm anterior to the kidney.

Together, the four included species in this subfamily manifest seriatim, from simple to complex, an impressive transition series in the basal male conduit from what surely is a pilaster to that which appears to be a verge or penis papilla. *Callistoplepa barriana* is the most primitive with an elongate, elevated pilaster on the ventral penial wall. In *C. shuttleworthi* the apical penis has permanently partially evaginated, pulling dorsally the basal-most part of the vas deferens into the pilaster and fixing it in place with tissue derived from the adjacent penial retractor. This progression is taken one step further in *Leptocala petitia*, wherein the permanently evaginated apical penis becomes so greatly enlarged, thick-walled and dorsoventrally distorted that the resultant pilaster essentially fills the thin-walled, sacular basal penis. Finally in *L. mollicella*, the pilaster assumes an apical position wherein it is axially pendulous within the thick-walled basal penis. At first glance, it appears to be a penis papilla, but the asymmetry within betrays the fact that it is in actuality a greatly modified pilaster. In all four species, the penial retractor is extremely short and inserts on the right columellar retractor. In *C. shuttleworthi* it inserts forward near the other branches; in the other species it inserts far to the rear. The penis sheath is so thin that it is difficult to trace; but it naturally enshrouds the entire penis, allowing the penial retractor and the vas deferens to pass out apically through the aperture of the sheath. A barely discernible transparent tissue layer attached directly on the surface of the penis is formed by the penial retractor. This may be the forerunner of the condition found in some Angolan achatinids, e.g. *Achatina welwitschi* Morelet, 1866, in which the penis is buried in dense muscle tissue extending from the penial retractor. Both the inner surface of the penis sheath and the adjacent but continuous outer surface of the penis are smooth, shiny and free from each other. This condition facilitates seriatim extroversion.

The spermatheca is consistently attached to the spermoviduct well above the junction of the apical vas deferens and the free oviduct. In the adult forms, there is no distinct vaginal retentor between the vagina and the body wall. In juvenile specimens of *C. shuttleworthi*, however, the anlage is present, which suggests that in this subfamily, its full development may be obviated by the highly developed, muscular basal female conduit.

Type genus: *Callistoplepa* Ancey, 1888.

Key to Genera

Sculpture of body whorl coarse, with slender, tightly and evenly placed prosocline costate ridges; shell aperture large, usually 52% of shell length; last whorl long, usually > 73% of shell length. Posterior foot with dorsolateral serrate ridges. No colored band on neck. Equatorial Guinea to Nigeria *Callistoplepa*
Sculpture of body whorl with extremely finely engraved microscopic rhomboids or vertical vermiculate granulae; shell aperture modest, usually > 52% of shell length; last whorl shorter, usually > 73% of shell length. Foot without dorsolateral ridges. Dark gray band on neck between ommatophores and mantle. Cameroon to western Zaire *Leptocala*

Callistoplepa**Callistoplepa**

Ancey, 1888:69 (footnote 2 for '*Achatina shuttleworthiana*' [sic = *A. shuttleworthi* Pfeiffer, 1856]); Pilsbry, 1905:viii, ix (fig. 2), xv (radula); Germain, 1909:90; Pilsbry, 1919:54, 60, 80, fig. 25 (map); Bequaert & Clench, 1934c:114; Ortiz & Ortiz, 1959:44; Zilch, 1959:372; Mead, 1986:144.

Ganomidos

d'Ailly, 1896:66. Type species by present designation, *Achatina barriana* Sowerby, 1890.

Callistoplepa

Ancey, 1898:92 (type species: *Achatina shuttleworthi* Pfeiffer, 1856); Thiele, 1929:560; Germain, 1936:151 (footnote 3); Verdcourt, 1966:111; Meredith, 1983:30; Oliver, 1983:9; Parkinson, *et al.* 1987:68; Vaught, 1988:90.

Ganomides

Boettger, 1905:170.

Ganomides

Verdcourt, 1966:111.

Callistoplepa s.s.

Mead, 1992.

After an extended trip to West Africa, a Captain Vignon prepared a catalogue of 104 land and freshwater molluscs that he had collected. The shells and the catalogue were subsequently acquired by a collector in Marseille and made available to his colleague C.F. Ancey, who was given the opportunity to publish this catalogue. Ancey (1888) agreed to present it 'such as it is, but with necessary, even indispensable, annotations because of defective identifications, some of which are not found to be at the level of the science' (*trans.*). In one of many footnote annotations, he placed '*Achatina shuttleworthiana*' [sic] under a new generic name '*Callistoplepa*'. If Ancey was not responsible for the misspelling of the specific name '*shuttleworthi*', then at least he did not correct it. The greater misfortune was that he misspelled the proposed generic name, which as revealed later (Ancey, 1898) was intended to be '*Callistoplepa*' (Gr. most beautiful robe).

In view of Ancey's casual manner of publishing the description of this genus, the spelling of the generic name '*Callistoplepa*' must be considered to be the 'correct original spelling' (ICZN Art. 32 (b) and is 'to be preserved unaltered'. According to Art. 32 (c), Ancey's name does not qualify as an 'incorrect original spelling' because, 'without recourse to . . . external source of information,' there is no 'clear evidence of an inadvertent error' even though orthographically it would have been desirable to have spelled it '*Callistoplepa*'. His unorthodoxy and failure to make a timely correction in spelling suggested that he was content for ten years to leave it in its original form. In the meantime d'Ailly (1896) unwittingly proposed the generic synonym *Ganomidos* including *Achatina shuttleworthi* along with *A. barriana*. Further, Ancey's original spelling contravenes no provisions of the Code articles. It is only in his belated publication (1898) that he used the spelling '*Callistoplepa*', without even implied justification for the change in spelling. Under the circumstances, this constituted an 'unjustified emendation' of the original spelling and therefore it is a junior objective synonym (Art. 33 (b)(iii)). Or, perhaps it was just another one of his regrettable misspellings. This rationale supports Pilsbry's conclusions (1905:126), but not those of Germain (1936:151

footnote 3). Unfortunately, the confusion about the valid spelling of the generic name has persisted in collections and even in the more recent literature, e.g. Parkinson *et al.*, 1987:68, Vaught, 1988:90. It is hoped that the present explanation finally will obviate any further confusion.

Ancey (1888) gave as the outstanding characteristics of this new genus its totally different appearance, thin shell, fine striation, and a colour pattern recalling *Orthalicus gallinasultana*. d'Ailly (1896) was the first to describe adequately this taxon, emphasizing the delicate, translucent, shiny, white-flecked shell, the vertical filiform sculpture, the mammillate apex, the inflated body whorl, the elongate, serrate-cristate foot, the hard-shelled eggs, and the unusual radulae of both *Ganomidos shuttleworthi* and the then, newly embraced *G. barriana*. Pilsbry (1905) accepted broadly d'Ailly's characterization of the genus and emphasized the importance of the very thin shell, the closely 'ribplicate' sculpture and the broad central tooth of the radula. In addition, he included in Ancey's genus *Callistoplepa*: *Ganomidos pellucidus* Putzeys, 1898, *G. fraterculus* Dupius & Putzeys, 1900, *Achatina marteli* and its subspecies *A. m. pallescens* Dautzenberg, 1901. Germain (1909) and Pilsbry (1919) retained this grouping. Bequaert & Clench (1934c) added to this genus on the basis of shell characters: *Achatina nyikaensis* Pilsbry, 1909 and *A. graueri* Thiele, 1911. In the present work it is demonstrated on the basis of the soft anatomy that the taxa added to *Callistoplepa* since d'Ailly (1896) are not congeneric, but are in subfamily Achatininae.

Bequaert & Clench (1934c:114) were misleading when they reported that *C. barriana* and *C. shuttleworthi* 'are from Upper Guinea'. Columbia Lippincott Gazetteer (1952) defines Guinea as equatorial West Africa from Senegal to Angola, being divided into Upper and Lower Guinea by the Niger Delta. van Bruggen (1989) supports the interpretation that the division is at the Dahomey Gap. In either interpretation, these species are limited to Lower Guinea. d'Ailly (1896:70) states that both species live in small numbers in shady places at the base of tree trunks and under detached pieces of bark.

Key to Species

Second whorl with thin crescentic threads and granules; last whorl evenly convex, expanding greatly, four times the length of the penultimate whorl when viewed dorsally; aperture length > shell width except in smallest specimens; peripheral arrow-shaped pattern usually pale and diffuse, occasionally absent or nearly so; the suture transects a smaller and often darker pattern; white flecks sparse or abundant, irregularly distributed; nepionic whorls 3; larger species (6 whorls = 38–52 mm long). Genital aperture complex, large, superficial; penial retractor inserts on the right columellar retractor posterior to all other branches; penis tubular; vagina longer than wide. Cameroon, Nigeria *barriana*

Second whorl grossly deeply closely and evenly costate; last whorl subcarinate, expanding proportionately, three times the length of the penultimate whorl when viewed dorsally; aperture length < shell width; conspicuous light castaneous arrow-shaped pattern at periphery, with concentrations of white flecks tending to alternate with the pattern; a smaller similar pattern appears subsuturally, but the white flecks there are more scattered; nepionic whorls 2½; smaller species (6 whorls = 26–34 mm long). Genital aperture simple, small, lacunate; penial retractor inserts on the right columellar

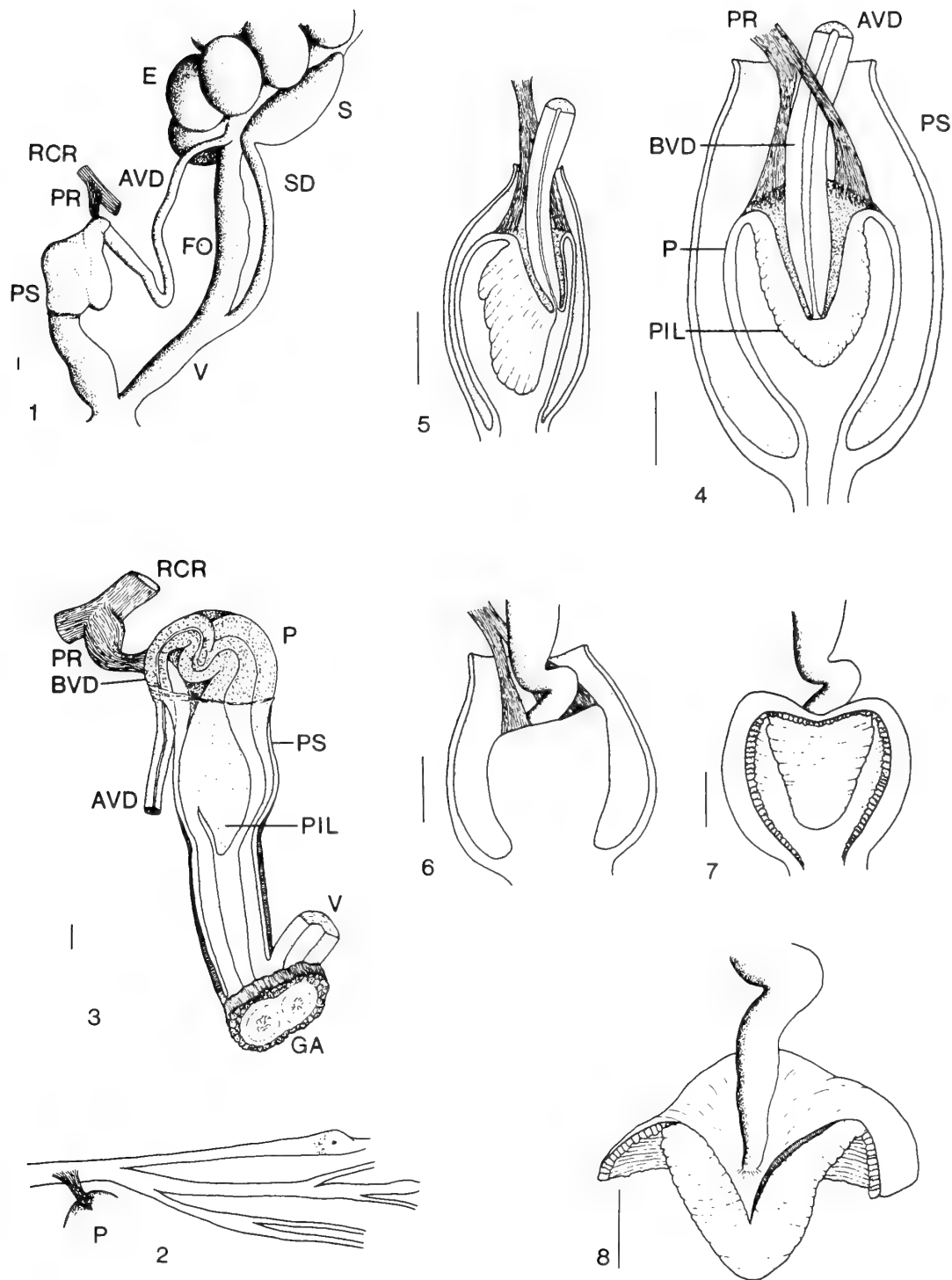


Fig. 1 *Callistoplepa barriana*, basal genital structures (MRAC no. 795.956).

Fig. 2 *C. barriana*, right branch of columellar muscle showing posterior attachment of the penial retractor.

Fig. 3 *C. barriana*, right ventrolateral view of penis to show the pilaster in profile. Contraction during preservation has telescoped the apical penis and forced it and its fibromuscular matrix out of the penis sheath.

Fig. 4 *Callistoplepa shuttleworthi*, penis sheath, permanently partially evaginated penis, and pilaster (containing the basal vas deferens) are shown in frontal plane and in dorsal view (UUZM).

Fig. 5 Same, in a slightly tangential sagittal plane.

Fig. 6 Same, in ventral view with penis sheath cut longitudinally and spread laterally to show the penis within.

Fig. 7 Same, with penis cut longitudinally and spread laterally to expose the pilaster within. Penis sheath not shown.

Fig. 8 Same, with pilaster cut and spread to reveal the basal vas deferens opening dorsally into the lumen of the penis. The dense fibromuscular webbing at the junction of the basal vas deferens and penis has been removed for clarity.

retractor anterior to the retractor of the right optic tentacle; penis permanently partially evaginated; vagina wider than long. Cameroon, Gabon, Equatorial Guinea ('Grand Bas-sam' locality is suspect) *shuttleworthi*

***Callistoplepa barriana* (Sowerby, 1890)**

Figs. 23, 24

Achatina barriana

Sowerby, 1890:579, pl. 56, fig. 2; von Martens, 1891:30.

Ganomidus barrianum

d'Ailly, 1896:70, pl. III, figs. 5–10 (egg), text fig. (radula).

Callistoplepa barriana

Pilsbry, 1904–05:127, pl. 47, figs. 14–17 (egg), pg. ix fig. 2, pg. xv (radula, ex d'Ailly); Germain, 1909:90; Bequaert & Clench, 1934c:114.

Ganomidus barrianum

Boettger, 1905:170.

Callistoplepa barriana

Dautzenberg, 1921:98; Oliver, 1983:9 (syntype).

SHELL. Shell ovate-conic, very thin, fragile, translucent, shiny. Whorls 6–6¼, rarely 6½, moderately convex. The second and third nepionic whorls are nearly straight sided, but they immediately give way to postmergent rapidly expanding whorls, producing a mammillate or submammillate, broadly conic spire and a blunt apex. Shallow sutures form a thin, nearly even line. Last whorl large, convex, 82% of shell length, range for 4–6½ whorls = 78–86% (n = 115), swelling faintly outward directly below the suture in some specimens. Aperture broadly ovate, nearly vertical, pale milky within. Columella thin, slender, slightly to broadly arcuate, concolorous, squarely to obliquely truncate, inner rim rolled adaxially. Outer lip thin, nearly evenly arcuate; joining the periphery at only a modestly acute angle; greatest width is characteristically midway. Parietal callus scarcely apparent in unweathered specimens.

From apex to base, the shell ground collar is uniformly pale fulvous. Superimposed on this, beginning imperceptibly in the fourth whorl, are two narrow bands of slender yellow-brown chevrons – one at the periphery, and a less distinct one transected by the suture. The chevrons in close juxtaposition have their apices oriented prosocline and are about as wide as the space between them. Much thinner, more irregular, paler, parallel sinuate stripes may join the two bands. Specimens with the most conspicuous patterns may have a second zone of thin, pale, transverse bands between the periphery and the base of the shell. The peripheral pattern tends to fade with increased growth. Some specimens may have present only the sutural band, or a unicolorous last whorl, or an entirely unicolorous shell except possibly for a slightly darker transverse band laid down between growth periods. Any of the whorls may be flecked with minute circular or elongate white spots (usually ca 0.2–0.8 mm). These are irregularly and sparsely dispersed, but are especially conspicuous within the costae of the last whorl. Upon close examination, they are seen to be a consolidated white powdery substance between the two periostracal layers. Although some are associated with shell injuries, their formation is apparently a natural phenomenon contributing to cryptic coloration.

The most apical portion of each nepionic whorl dips abruptly at near-right angles adaxially to form a narrow platform in which is embedded a strikingly uniform series of minute shallow pits that fringe the suture. This ornamenta-

tion is limited to the nepionic whorls and is the homologue of the diagnostic grossly costate sculpture in the second nepionic whorl of *C. shuttleworthi*. The first whorl is essentially smooth. Short faint slender crescentic threads and granules, oriented transversely but aligned spirally in irregular series, gradually make their appearance in the second whorl. As this sculpture becomes more organized, the spaces between the several spiral series seem to form shallow spiral striae. Near the junction of the third and fourth whorls, a sharp transverse delineation marks the end of the nepionic whorls, at which level the threads become more symmetrical and greatly compressed, but retain their individuality. With continued growth, the threads remain fairly distinct or become transversely variously fused into costellae, which interrupt or obliterate in part the shallow spiral striae. Gradually the threads become more bold and evolve into slender, closely and very evenly placed prosocline corrugations or costae, commonly with splitting and anastomosis. The spiral striae remain superficial, barely transecting the costae. The depressed cancellate sculpture below the periphery of the upper whorls gradually becomes more corrugate until an essentially uniformly costate sculpture is finally formed on the entire forward last whorl of the fullgrown specimen, diminishing slightly toward the columella and obliterating the peripheral line of demarkation. The smallest shells may be vaguely subcarinate.

SOFT ANATOMY. Alcohol preserved specimens available 31/dissected 13. Nigeria: BMNH 1/1; Cameroon: MRAC 2/2, SMNH 10/4, SMF 14/6, UUZM 4/0. d'Ailly (1896) had access to 34 alcohol-preserved specimens collected in Cameroon by P. Dusén, Y. Sjöstedt and J.R. Jungner. With the generous assistance of Dr Åke Franzén, a diligent search was made in the museums of Stockholm and Uppsala in 1987, but only 14 specimens could be found. There was no evidence of Jungner's specimens.

The body of the preserved specimen is uniformly grey fulvous, without any apparent markings. Immediately posterior to the shell, there is a depressed plateau that is fringed by two prominent dorsolateral ridges, each composed of 12 closely aligned, truncate incisor-shaped elevations.

The most unusual feature of the internal anatomy of this species is the penis sheath (PS) (Fig. 1). Thickest at its base (~0.5mm) it diminishes apically to a diaphanous fascia (~0.05 mm) that, in the normal position, enshrouds the apical penis (P), the most basal part of the vas deferens (BVD), and the basal portion of the extraordinarily short penial retractor (PR). As in other achatinids, the origin of the PR marks the division between P and BVD. In contrast to that in *C. shuttleworthi*, the PR inserts on the right columellar retractor (RCR) posterior to all other branches (Fig. 2). In the fully mature specimen (Fig. 1) the tapering attenuated apical P appears to be cramped into a sigmoid fold in this thinnest apical PS. A dense webbing of muscle and connective tissue fibrils, originating from the PR, obscures, entangles and foreshortens the apical folds of the P, even to the point in the oldest specimens where this tight, woolly mass of fibromuscular tissue becomes histologically intimately intermeshed with the substance of the apical penial wall. On its outer surface, this cocoon-like network forms a smooth, dense coating over the P that is completely free from the equally smooth but very shiny inner surface of the PS, thus allowing free movement between P and PS. Basally, where the PS is thickest, this fibrous layer conversely becomes so

thin on the surface of the P and so intricately associated with it, as to be essentially imperceptible. About midway on the P, the PS suddenly goes from thick to thin. This creates a transverse line of thin folds that incorrectly suggests the PS terminates at that level (Mead, 1992, fig. 2). However, when there is extreme contraction during preservation, the apical edge of the PS actually does pass basally far enough to allow the apical structures to elbow out of the PS (Fig. 3). The contraction emphasizes the bipartite nature of the P: an apical convoluted, transparently ensheathed portion and a basal irregularly bulging, opaquely ensheathed portion that contains the pilaster (PIL). Internally, the most basal P is longitudinally plicate; above that, including the PIL, the epithelium is vermiculate-rugate. The PIL is a simple, greatly thickened, longitudinal, roundly elevated ridge of the ventral penial wall that strongly projects dorsally into the lumen of the P. Basally, this ridge terminates into a solid, inverted-conical, pendulous verge-like process. Although its margins are not well defined, axially the PIL has a more gross epithelial texture than the surrounding tissue. The apical vas deferens (AVD) is a conspicuously uniformly slender conduit (~1.0 mm in width). It lacks the heavy muscular basal portion found in *C. shuttleworthi*, thus the physical support for the intromittent organ in *C. barriana* doubtless is provided by the thick, longitudinal P.

The vagina (V) is a short, nearly uniformly wide conduit, about one-third the length of the P. Internally, it is lined with vermiculate-rugate epithelium and is without any apparent modifications at its junction with the spermathecal duct (SD) and free oviduct (FO). The muscular FO is as wide or wider than the V, 2–3 times as wide as the SD, and about as long as the SD. For their full length, both FO and SD are tightly bound to each other by fairly regularly appearing small slips of muscle. The junctions of the AVD/FO and spermatheca (S)/SD are pulled in close juxtaposition by the tissues of the sagittal myoseptum. Just apical to this, the capitate S, about the length of the V, is broadly attached to the basal (uterine) portion of the spermooviduct. The SD is a thin-walled mostly uniformly slender conduit about the caliber of the AVD. Five gravid specimens were examined; three with full data had been collected near the end of the rainy season in October/November. For such a relatively small species, the eggs are quite large (6.8×5.4 – 6.3×5.1 mm). Fully gravid specimens contained 11–15 eggs, all with heavy, calcareous shells and distributed in the full length of the spermooviduct. The ovotestis acini appear in four or five discrete clusters under the columellar surface of the right (apical) lobe of the digestive gland. A talon with a round base and an apical, diverticulate elongation is present.

The genital atrium (GA) in this species is unique among the achatinids so far dissected. It is comparatively large and so shallow that it is essentially a common genital depression, immediately within which appear conspicuously the male and female orifices. These latter, like twin craters, are individually surrounded by low elevated circular walls of smooth tissue, which contiguously fuse at their inner margins (Fig. 3).

TYPE MATERIAL. Sowerby (1890:579) did not designate a holotype. The BMNH specimen '89:11.19.2 purchased of Sowerby' is here designated the lectotype (Figs. 23, 24; Table 1). The slightly damaged and trimmed second syntype, NMW, 1955:158.832 in the Melvill-Tomlin collection is here designated a paralectotype (Oliver, 1983). Remeasurements

of the lectotype confirm Sowerby's figures except for the shell length, which is 41.0 mm rather than '43 mm'. Sowerby's illustration is so poorly rendered that it is not precisely identifiable with either syntype.

TYPE LOCALITY. 'Calabar, Africa?' Nigeria, 4° 57' N, 8° 19' E. J.C. Reid of the University of Calabar recently confirmed this queried locality. Although he has made many excursions into the 'relatively undisturbed Oban Hills Forest which yields a rich fauna', he found only two (live) specimens along a permanent stream at Aking (= Awsawmba) 5° 26' N, 8° 38' E, 78 km northeast of Calabar. One of these specimens (BMNH) was examined anatomically and conchologically in the present study and was found to be typical; the second specimen is reportedly in the Tom Pain collection (NMW).

DISTRIBUTION. This species has been found essentially along the entire expanse of coastal Cameroon from M'Bonge (= Bonge) 4° 33' N, 9° 05' E in the north to Itoki 2° 24' N, 9° 50' E in the south. Most of the known twenty localities are clustered in northwestern Cameroon, spilling over into southeastern Nigeria and extending inland as far as Yaoundé 3° 52' N, 11° 31' E; Métet 3° 05' N, 11° 00' E; Ebolowa 2° 54' N, 11° 09' E and Sangmélima 2° 56' N, 11° 59' E. The nine other localities are in the environs of Victoria 4° N, 9° E. In all localities, seven were shared with *C. shuttleworthi* and five were shared with *Leptocala mollicella*. Only a single general locality record was found for Gabon (Verreaux, 1855 NHMB) and no record for Equatorial Guinea; but this species eventually probably will be found to be limited to the northern regions of these two countries. Data labels indicate that specimens were collected in plantations in Kumba 4° 38' N, 9° 25' E (bananas), Missellele 4° 07' N, 9° 25' E (coca), 'Buenga' (oil palm), and in primary forests.

Table 1 *C. barriana* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Width	% whorl	% LW/L	% W/L	
6¼	59.0	32.4	36.1	19.5	49.0	82	55	Bonge (UUZM)
6¼	57.5	30.0	32.8	16.9	46.0	80	52	Victoria (ZMB)
6	50.7	27.8	30.9	16.8	41.9	83	55	Idenau (SMF) [†]
6	49.0	29.9	30.6	17.5	40.8	83	61	Bonge (SMNH)
5¾	44.0	27.4	29.6	16.3	37.8	86	62	Bonge (SMNH)
6	41.0	23.3	24.9	14.5	32.3	79	57	Calabar (BMNH) Lect <i>A. barriana</i> *
6	41.0	22.8	26.6	13.4	34.0	83	56	Kumba (MRAC) 795.173
5½	36.8	23.0	23.6	13.4	29.8	81	62	Idenau (SMF)
5	25.2	15.3	16.4	8.8	20.6	82	61	Bibundi (SMF)
4¾	20.5	13.8	13.2	7.6	16.8	82	67	Bibundi (SMF)

Total specimens examined: 125. Sources: BMNH, CMNH, IRSN, MCZ, MNHN, MRAC, NHMB, NHMW, NMW, SMF, SMNH, UHZI, UUZM, ZMB, ZSM.

REMARKS. This species is commonly encountered in collections and often confused with immature *Achatina bandeirana* Morelet, 1866 and *A. craveni* E.A. Smith, 1881, both of which have a proportionately much smaller last whorl.

***Callistoplepa shuttleworthi* (Pfeiffer, 1856)**

Figs. 25, 26

Achatina shuttleworthi

Pfeiffer, 1856:34, 1859:603, 1868:216, 1877:275.

Callistoplepa shuttleworthiana

Ancey, 1888:69.

Ganomidos shuttleworthi

d'Ailly, 1896:69, pl. 3, figs. 11–14, text fig. (radula).

Callistoplepa shuttleworthi

Ancey, 1898:92; Thiele, 1929:560, fig. 644 (radula).

Callistoplepa shuttleworthi

Pilsbry, 1904–05:127, pl. 47, figs. 18–20, pg. xv (radula, ex d'Ailly); Germain, 1909:90, 1916:248, pl. 10, fig. 4; Bequaert & Clench, 1934b:114; Ortiz & Ortiz, 1959:45, pl. 5, figs. 97, 98, text figs. 28–31 (genit. syst., pallial complex, jaw, radula); Zilch, 1959:373, fig. 1352.

Ganomidos shuttleworthi

Boettger, 1905:170.

SHELL. Shell elongate-ovate, extremely thin, very fragile, translucent with a subdued gloss. Whorls $5\frac{1}{2}$ – $5\frac{3}{4}$, rarely 6, noticeably flattened in profile. A somewhat restricting, deeply cut second nepionic whorl produces a mammillate obtuse apex. The following whorls form a slender conic spire as they descend more rapidly than they expand. Sutures between nepionic whorls are deep and regular; those between postemergent whorls are more shallow and only slightly irregular. Last whorl subcarinate, noticeably so in juvenile specimens, expanding proportionately, 77% of shell length, range for $4\frac{1}{2}$ –6 whorls = 73–83% (n = 60). Aperture oblique-ovate, external colour pattern sharp and distinct from within. Columella usually straight, axial, rarely slightly arcuate, inner rim erect with a cord-like thickened crest; truncation oblique to very oblique, rarely at right angles. Between the third and fourth whorls, the crest of the columella rolls abaxially on itself to form a hollow tube, therefore an open umbilicus. Between the fourth and fifth whorls, this tube narrows and solidifies to form a slender axial cord, which is seen in the full grown shell. This series of changes, from open to closed, enigmatically has been observed in several disparate achatinid species, e.g. *A. achatina* (Linné, 1758) and *Archachatina* spp. Outer lip of shell thin, skewed basally, joining the periphery at an acute angle; greatest width below midway; this is emphasized by the subcarinate nature of the shell. Parietal callus thin, vague.

Shell ground colour is pale corneous. The first $2\frac{1}{2}$ whorls are unicolorous. Starting near the third whorl, vague roundish, very pale castaneous spots appear both at the suture and periphery. At these two levels, the spots quickly assume sharply angulate prosocline arrow-shaped patterns, highlighted with a series of parallel transverse elongate white flecks. Similar flecks, reminiscent of those in *C. barriana*, are scattered irregularly over the shell above the periphery, rarely below. Soon the sutural band fractionates and moves increasingly into a subsutural zone. The large arrows at the periphery become spirally closely juxtaposed to form an essentially continuous dominating colour band. From it, slender, nearly parallel light castaneous stripes pass sinuously

to the subsutural band and transversely to the columella.

Only rudimentary costae appear in the last part of the otherwise smooth first whorl. The entire second whorl is conspicuously and uniformly ribbed from suture to suture with elevated, deeply cut, nearly orthocline, gross costae, ca 0.2 mm wide (cf Germain, 1916 pl. 10, fig. 4). In the third whorl the now more prosocline costae are soon reduced to half their width. At midway in this whorl, an interruption in the alignment of the costae marks the end of the nepionic whorls. Gradually the costae become wider and finally regain their original width in the fifth whorl, only to become narrower and somewhat irregular in the last part of the sixth whorl. Faint shallow closely spaced spiral lines, starting in the second whorl, almost imperceptibly transect the prominent costae. There is a delicate, greatly suppressed cancellate-granulate sculpture on a vitreous surface below the periphery in the upper whorls. This is invaded by the costae in the sixth whorl until the entire whorl from suture to columella is nearly uniformly costate. No splitting or anastomosis of the costate has been observed.

SOFT ANATOMY. Alcohol preserved specimens available 12/dissected 5. Cameroon: SMNH 5/2, UUZM 7/3. All specimens were collected by Y. Sjöstedt. The only two extant mature specimens were found by Å. Franzén in a medical laboratory at UUZM. d'Ailly (1896) reported having access to 11 alcohol preserved specimens, which apparently did not include Sjöstedt's Itoki specimens that were available in the present study.

Body colour as in *C. barriana*; spade-shaped elevations on the posterior foot only slightly less prominent.

Without having dissected and deciphered first the relatively more simple reproductive tract of *C. barriana*, it would have been very difficult to interpret the relationships of the genital structure in this species. In essence, the axis of the basal male conduit has been greatly foreshortened telescoping the homologous structures to such an extent that the pilaster (PIL) on the ventral wall of the penis (P) is pivoted 180° , forcing the junction of the P and basal vas deferens (BVD) deeply into the dorsal aspect of the infolded P, i.e., the upper ventral wall of the P and the most basal part of the BVD are therefore seen only in the dorsal or lateral views (Figs. 4, 5). A dense network of muscle and connective tissue fibrils firmly fixes the structures in this permanently partially evaginated position. This places the aperture of the BVD and the contiguous subapical part of the PIL into a basal position within the folded penial wall to take the lead in forming the intromittent organ at extroversion. The inner smooth shiny surface of the extremely thin-walled penis sheath (PS) facilitates seriatim extroversion: PIL-P-PS and finally genital atrium, with the BVD and the attenuated penial retractor (PR) contained axially within the intromittent organ. Figures 6, 7, 8 show at progressively deeper levels of dissection these relationships from the ventral view. Both PIL and the inner penial wall are confluent with a deeply rugate epithelium. It should be noted that since the BVD opens directly into the lumen of the penial chamber rather than passing through the accessory organ to open at its apex, a pilaster rather than a verge (penis papilla) is formed.

The PR is extremely short and, as in the other species of Callistoplepinae, it and the BVD are held tightly together by the PS apical to the completely enclosed P (Fig. 9). In contrast to that in *C. barriana*, the PR inserts on the right columellar retractor (RCR) anterior and strongly ventral to

the retractor of the right ommatophore (RRO) (Figs. 10, 2). Ortiz & Ortiz (1959) missed the diminutive PR in their dissections and do not show it in their illustrations. Emerging above the PS, the apical vas deferens (AVD) is a large muscular thick-walled conduit that in its normal position reaches to the penio vaginal angle and doubtless serves both as an ejaculatory duct and a physical support for the intromittent organ. Apical to this, the conduit narrows to half the calibre and is thinner walled.

The vagina (V) is very short, but two to four times wider than its length. Near its base, sparse, thin muscle strands suggest a primordial vaginal retentor. Internally, the V is muscular, thick-walled and longitudinally deeply plicate. There is no sharp delineation between it and the broad, somewhat thinner walled basal spermathecal duct (SD). This latter is so large that it tends to be positioned partly between P and V. Both upper SD and free oviduct (FO) are thin-walled and of about the same calibre. The clavate spermatheca (S) is broadly attached to the spermoviduct apical to the AVD/FO junction. The ovotestis acini are as in *C. barriana*. No specimen was found to be gravid, but a single specimen collected in October in Bonge seemed to be near it with a very large albumen gland and an inflated spermoviduct. Ortiz & Ortiz (1959) examined a single specimen from Fernando Póo Island (Macías Nguema Biyogo) and found the spermoviduct completely crowded with four comparatively large white eggs. Seven dried eggs (MCZ no. 219224) measured in the present study average 4.7×3.7 mm. A diminutive talon is present. In contrast to *C. barriana*, the genital atrium is an inconspicuous dimple without superficial embellishments.

TYPE MATERIAL. Pfeiffer (1856) described this species from Cuming collection specimens, giving the shell size as $5\frac{1}{2}$ whorls and the length-width measurements as 34×17 mm; later (1859) he gave aperture measurements as 19×11.5 mm. The measurements of the three syntypes in BMNH do not match those of Pfeiffer, but are reasonably close. The largest syntype has a damaged and repaired last whorl and the next largest is atypically slender; therefore the smallest specimen (Figs. 25, 26; Table 2) is here selected as the lectotype, the other two becoming paralectotypes. No convincing evidence was found that other syntypes are extant. Only four other specimens of the 60 examined in the present study exceeded 30 mm in shell length.

TYPE LOCALITY. The syntypes in the Cuming collection were reported to be from "Grand Bassam" *Africae occidentalis* (Verreaux). All other specimens examined bearing this locality were sold by shell dealers, viz. Da Costa, Fulton, Geret, Paetel and Preston, who may have taken their cue for a locality from the original description. No museum specimen has been found with a locality record from the 1400 km stretch of continental Africa between Grand Bassam, Ivory Coast and the cluster of reliable locality records in northwest Cameroon. It is suspected that this is a case of still another erroneous Cuming record. Although under the circumstances, we must accept the type locality as 'Grand Bassam', it is probable that Cuming's specimens came from Cameroon, or perhaps Gabon. The likelihood of an early secondarily established population in Grand Bassam prior to 1856 is extremely remote, for surely authentic collecting records would have appeared in the meantime. Edouard Verreaux (cf Crosse & Fischer, 1869) not only collected the syntypes of this species, but he also collected the single known specimen

Table 2 *C. shuttleworthi* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl	% LW/L	% W/L	
6	34.0	18.7	18.4	10.3	26.4	78	55	'G. Bassam' (MCZ) 83441
6	32.3	18.4	18.4	10.0	24.5	76	57	'G. Bassam' (BMNH) PLec
6	31.0	16.7	16.4	9.0	22.8	73	54	'G. Bassam' (BMNH) PLec
$5\frac{3}{4}$	30.9	18.3	17.0	10.7	24.0	78	59	'G. Bassam' (BMNH) Lect A. <i>shuttleworthi</i> *
$5\frac{3}{4}$	26.9	15.8	14.8	8.0	20.7	77	59	Edea (MCZ)
$5\frac{1}{2}$	24.1	14.8	14.4	8.0	19.0	79	61	Gabon (MRAC) 5314 (Preston)
$5\frac{1}{2}$	22.9	13.0	12.1	6.8	17.3	75	57	Bibundi (SMNH)
$5\frac{1}{4}$	20.2	11.5	11.8	6.8	16.1	80	57	Itoki (UZZM)*
5	19.4	11.4	11.2	5.9	15.4	79	59	Bibundi (SMF)
$4\frac{1}{2}$	16.0	10.5	8.9	5.3	12.5	78	66	Gabon (IRSN) (Vignon)

Total specimens examined: 60. Sources: BMNH, GNM, IRSN, MCZ, MNHN, MRAC, NHMW, SMF, SMNH, UMMZ, USNM, UZZM, ZMB.

of *C. barriana* from Gabon, now in Bern (NHMB). This raises the suggestion that Verreaux, after collecting in Gabon and Cameroon, shipped his specimens from Grand Bassam, which Cuming assumed was the collecting site.

DISTRIBUTION. Leonardo Fea was the first to discover this species on Fernando Póo Island (= Macías Nguema Biyogo) of Equatorial Guinea $3^{\circ} 30' N$, $8^{\circ} 40' E$ (Germain, 1916:249). Subsequently, Ortiz & Ortiz (1959:45) reported it from Basilé and Mongola on that island. Nine reliable localities on the mainland in Cameroon define a limited coastal belt, ca 280×120 km with N'dian $4^{\circ} 55' N$, $8^{\circ} 53' E$ in the north; Méfét $3^{\circ} 05' N$, $11^{\circ} 00' E$ in the east; and Itoki $2^{\circ} 24' N$, $9^{\circ} 50' E$ in the south. Other Cameroon localities: Albrechts Höhe $4^{\circ} 38' N$, $9^{\circ} 25' E$; Mukonje (= Mukonye) $4^{\circ} 37' N$, $9^{\circ} 30' E$; Bibundi $4^{\circ} 13' N$, $8^{\circ} 59' E$; Edéa $3^{\circ} 48' N$, $10^{\circ} 08' E$; Lokoundje $3^{\circ} 13' N$, $9^{\circ} 55' E$. A specific locality record for Gabon was not found, but Vignon, through Ancey (1888:69), reports them as rare in Gabon at the edge of forest streams. They probably do not extend south of the Ogooué River.

Callistoplepa tiara Preston, 1909 – A Misidentification

Preston (1909:183, pl. vii, fig. 9) described *Callistoplepa tiara* from 'Bitze [= Bitye], near the River Ja [Dja], Cameroons' ($3^{\circ} 01' S$, $12^{\circ} 22' E$). He indicated neither the collector nor the number of specimens he had; however, some specimen labels (BMNH, MRAC) specify that G.L. Bates was the collector. Between 1908 and 1912, Preston distributed ten known syntypes, each bearing the full locality information

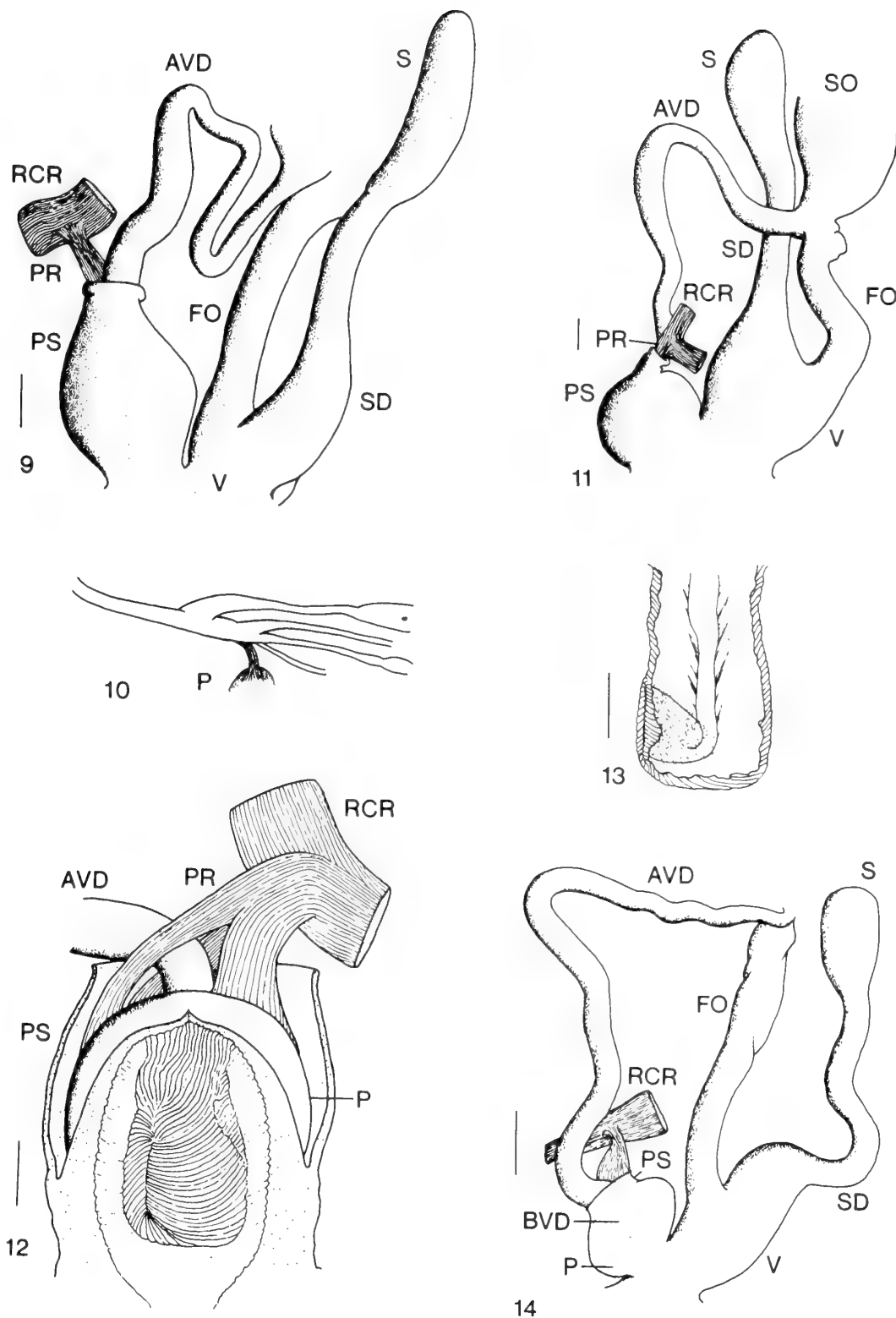


Fig. 9 *C. shuttleworthi*, basal genital structures (UUZM).

Fig. 10 *C. shuttleworthi*, right branch of columellar muscle showing anteroventral attachment of the penial retractor.

Fig. 11 *Leptocala mollicella*, basal genital structures (MRAC no. 796.850).

Fig. 12 *L. mollicella*, penis sheath, penial retractor and penial wall cut longitudinally and spread to reveal the pendulous pilaster within (MRAC no. 795.638).

Fig. 13 Same, cutaway of pilaster to show basal vas deferens joining the penial sacculus, which leads to the aperture of the pilaster.

Fig. 14 *L. petitia*, basal genital structures (MRAC no. 214.044).

and Preston as the source. These syntypes are currently to be found in the following museums: BMNH (3: no.1908.7.1.13-14, and MacAndrew Coll.), NMW (Melville-Tomlin Coll. no.1955.158.826; Oliver, 1983:1), IRSN (Dautzenberg Coll. no.169), ZMB (no.62345), MNHN, MRAC (no.5760), RMNH, UMMZ (Bryant Walker Coll. no.142031). These vary in size from $6\frac{1}{2}$, 63.0×31.3 to $5\frac{1}{2}$, 44.2×25.7 . Preston probably placed his presumed new species in *Callistoplepa* because of the very thin shell, the Cameroon type locality, and the fact that the size, general shape and peripheral colour pattern of his specimens were reminiscent of *C. barriana*. However, upon examination of the shell sculpture in the present study, all syntypes were found to be juvenile *Achatina bandeirana* Morelet, 1860.

In Cameroon, *A. bandeirana* and the closely related *A. iostoma* Pfeiffer, 1854 and *A. balteata* Reeve, 1849 are sympatric and it is not uncommon to find mixed lots of these three species in museum collections. Preston, himself, apparently had a mixed lot from which his syntypes were selected. He sent a 'cotype' of *Callistoplepa tiara* to Dupuis (IRSN, General Coll.); however, its locality record was simply 'Cameroon'. After Dupuis (1923) examined this specimen, he concluded that it probably was a juvenile *A. iostoma*. In 1934, Bequaert also saw this specimen and confirmed Dupuis' conclusion. Their identifications were corroborated in the present study because this 'cotype' specimen revealed the following characters in contrast to those of the syntypes identified as *A. bandeirana*: 1) upper whorls not convex, but form a nearly straight-sided pyramid; 2) apex more acute rather than blunt; 3) a slight but apparent peripheral carina is present in the early whorls; and 4) sculpture is formed by finer, more uniform, elevated beads that do not evolve into minute prosocline arcuate welts in the sixth to seventh whorls (cf Bequaert & Clench 1934a fig. 3). This last character is diagnostic for *A. bandeirana*; but it is inadequately developed in the very immature specimen of five to six whorls, thus such individuals of the three species may appear to be alike.

Dupuis' unique 'cotype' persuaded Bequaert to assume that all syntypes of *C. tiara* were juvenile *A. iostoma* and he so identified them in collections (BMNH, IRSN, ZMB, RMNH) and in his publications (Bequaert, 1950:39; B. & Clench 1934a:13; 1934c:114). Dautzenberg was similarly impressed and was moved to place with his 'cotype no.169' an added notation, 'Erreur de Preston, C'est un jeune *Achatina iostoma* Pfeiffer'. This was unfortunate because Dautzenberg's specimen, with full *C. tiara* field data, is shown now to be an immature *A. bandeirana*. IRSN thus has a true syntype in the Dautzenberg Collection and questionable 'cotype' in the General Collection, which latter is here confirmed to be *A. iostoma* and not a bona fide syntype. A somewhat similar situation exists at BMNH, which has three valid syntypes. A fourth specimen in the Connolly Collection (BMNH no.1937.12.30.3684) was sent by Preston and labelled '*Callistoplepa tiara* Pr.' (apparently in his writing) but without any locality data, except 'Bitz' in the accession book. Connolly had his doubts about the identification and relabelled it '*Achatina ? balteata* Rve juv.' Bequaert also saw it in 1933 and referred to it as *A. iostoma*. This now proves to be still another juvenile *A. bandeirana* and is here considered a doubtful eleventh syntype of *C. tiara*.

It should be noted that *A. bandeirana* is a wide spread, highly variable Lower Guinea species complex involving *A. b. arenaria* Crowley & Pain, 1961; *A. b. mayumbensis* C. & P., 1961; *A. paivaana* Morelet, 1866, (1868); and *A. dohrni-*

ana Pfeiffer, 1870. It is found from Cameroon to northern Angola (7° N– 10° S) and fans north and east into Gabon, Central African Republic, Congo Republic and Zaire. A study of this complex is in progress.

Preston did not designate a type, but he retained in his own collection the specimen that was illustrated in his description of this species. This syntype is here selected as the lectotype (measurements: 6; 49.4×26.7 ; aperture 30.9×13.8 ; last whorl 40.0 mm). It is now in Tervuren (MRAC no.5760) and can be precisely identified by the unique configuration of the map-like pattern on the last whorl. This pattern is caused by the irregular lifting up of the thin outer periostracal layer from the durable inner periostracal layer, allowing an air space between. This produces blotchy grey-white patches, which probably provide cryptic coloration. The juvenile and mature specimens of both *A. bandeirana* and *A. iostoma* commonly have these patches, which have been referred to as 'hydrophanous streaks' (Bequaert & Clench, 1934a:15). They apparently are homologous to the conspicuous white flecks on the shells of *Callistoplepa barriana* and *C. shuttleworthi* and may have contributed to Preston's decision to put his species in this genus.

Leptocala

Petitia

Joussemaume, 1884:171 (non Chitty, 1857); d'Ailly, 1896:71; Bequaert, 1950:138 (type species: *Petitia petitia* Joussemaume, 1884).

Leptocala

Ancey, 1888:70, 1898:92 (type species: *Achatina mollicella* Morelet, 1860); Thiele, 1929:560; Bequaert & Clench, 1934c:116; Ortiz & Ortiz, 1959:24.

Achatina (*Leptocala*)

Pilsbry, 1904:72; Spence, 1928:213; Bequaert, 1950:138; Zilch, 1959:366; Vaught, 1988:89.

Achatina (*Leptocola*)

Kobelt, 1910:66 (non Gerstaecker, 1883).

Leptocala (*Leptocala*)

Bequaert & Clench 1934b:272.

Pilsbry (1904:73, 75) reduced genus *Leptocala* to subgeneric rank in *Achatina* and placed within it his new Section *Leptocallista*. Thiele (1929:560) returned Ancey's *Leptocala* to generic rank and retained within it Sections *Leptocala* and *Leptocallista*. Bequaert & Clench (1934b:274) elevated these sections to genus and subgenus, respectively. In 1950, Bequaert placed both names as subgenera of *Achatina*. Zilch (1959:366) followed suite. The present studies of the soft anatomies demonstrate that these two genus-group taxa are in separate subfamilies because the East African *Leptocallista* is anatomically allied to *Lissachatina* and therefore is an achatinine.

Bequaert & Clench (1934b,c) announced that the Cameroonian *Pseudoglessula efulensis* Preston, 1908 might belong to *Leptocala* and stated that the type could not be located in the British Museum. The holotype (no.5309) and the paratype (no.97435) of this species were found during the present study in Tervuren (MRAC) and clearly proved to belong to the Subulinidae. Ancey (1888:71) incorrectly placed *Achatina polychroa* Morelet, 1866 in *Leptocala*; Bequaert (1950:48) believed it belongs in subgenus *Pintoa* of *Achatina*. A final decision depends upon a study of its soft anatomy.

The ancestral stock of the two closely related, remaining species in this genus, *L. mollicella* and *L. petitia*, probably became separated in fairly recent times by a vicariance event – possibly the development of the Ogooué River.

Because of the unique microsculpture and the somewhat smaller shell aperture, *Leptocala* up until now has escaped suspicion of being closely related to *Callistoplepa*. The genus is limited to the southwestern portion of Lower Guinea from northwestern Cameroon to far western Zaire.

Key to Species

Shell 6–6½ whorls; spire conic; exceedingly fine distinct vertical and spiral lines form shallow minute engraved rhomboids. Pilaster verge-like, cylindrical, vertically suspended from the apex of a dome-shaped penis; basal vas deferens obscured by penial retractor. North of Ogooué River in Gabon, Equatorial Guinea, Cameroon and probably south-eastern Nigeria *mollicella*
 Shell 6½–7 whorls; spire slender conic; exceedingly fine closely appressed vertical vermiculate-granulate sculpture obliterates the spiral lines, especially on the upper whorls. Pilaster potato shaped, somewhat compressed, attached for nearly its full length along a diagonal right ventrolateral axis of a hull shaped penis; basal vas deferens conspicuous in ventral view. South of Ogooué River in Gabon, Congo Republic, western Zaire and probably Cabinda, Angola *petitia*

Leptocala mollicella (Morelet, 1860)

Figs. 27, 28

Achatina mollicella

Morelet, 1860:189; Pfeiffer, 1868:216; 1877:275; Vignon (in Ancy, 1888:70); Pilsbry, 1904:29.

Achatina pulchella

von Martens, 1876:258, pl. 3, figs. 1, 2 (syntype) (*non* Spix & Wegner, 1827; *non* Pfeiffer, 1857); Ancy, 1888:70; Pilsbry, 1904:73, pl. 34, fig. 14 (ex von Martens).

Leptocala mollicella

Ancy, 1888:70, 1898:92; Thiele, 1929:560; Bequaert & Clench, 1934b:273.

Achatina smithi

Sowerby, 1890:579, pl. 56, fig. 3 (holotype, monotypy; *non* Craven, 1880).

Achatina sowerbyi

E.A. Smith, 1890:392 (new name for *A. smithi*).

Petitia pulchella

d'Ailly, 1896:71; Boettger, 1905:170.

Achatina (Leptocala) mollicella

Pilsbry, 1904:73; Spence, 1928:213, pl. 2, fig. 5; Bequaert, 1950:138; Zilch, 1959:366, fig. 1342.

Achatina (Leptocala) pulchella

Germain, 1916:154, 241, pl. 6, figs. 11, 12.

Leptocala (Leptocala) mollicella

Bequaert & Clench, 1934b:273.

Leptocala mollicella zenkeri

Bequaert & Clench, 1934c:118, pl. 1, figs. 5–7, pl. 2, fig. 13 (holotype, 3 paratypes).

Leptocala mollicello zenkeri

Bequaert & Clench, 1934c:119 (*lapsus calami*).

Achatina (Leptocala) mollicella petitia

Bequaert, 1950, pl. 58, fig. 4.

Achatina (Leptocala) mollicella zenkeri

Bequaert, 1950:138.

Leptocala pulchella

Ortiz & Ortiz, 1959:25, pl. 5, fig. 99.

SHELL. Shell obovate, glossy, translucent, thin but sturdy; periostracum tenaceous. Whorls 6–6½, moderately convex. Spire conic; apex broadly obtuse; sutures moderately deep, fine, straight or slightly irregular. Last whorl expanding at a somewhat greater rate than the upper whorls, 72% of shell length, range for 4¾–6½ whorls = 69–75% (n=34). Aperture elongate inverted ear-shape, pale milky within. Columella short, variably straight to slightly arcuate and twisted, transversely to obliquely truncate, basal crest slightly elevated in juvenile specimens. Outer lip thin, joining the periphery at a broadly acute angle. Parietal callus minutely granular, shiny, concolorous.

Shell ground colour is pale fulvous, rarely somewhat darker. Most specimens have a distinct but subdued pattern of pale yellow-brown, slender, strongly parallel, nearly straight or somewhat sinuous stripes, usually 0.2–0.3 mm wide, alternating with ground colour bands of about the same width. The banding may be slightly coarser and more conspicuous in the fifth whorl and above. Often apparently unicolorous or weathered specimens under proper lighting and magnification will be seen to have this characteristic pattern at least in limited areas. This is witnessed in Bequaert & Clench's (1934c) figure 7 of their *Leptocala mollicella zenkeri*, which they report is 'without any darker markings'.

The first 1–1½ whorls are smooth and very shiny. Short vertical or arcuate lines begin to appear in the second whorl, often concentrated at the suture below. These soon elongate into delicate, narrow, closely packed vertical lines that span the full width of the whorl. At 2½ whorls, there is a conspicuous diagonal demarkation between the nepionic and the postemergent whorls. At this demarkation, spiral lines that immediately previous to this were sparse, short and ghost-like, quickly form 35–40 nearly evenly spaced exceedingly shallow, but sharply engraved lines. These lines cross the vertical lines and cut the surface into minute engraved rhomboids (see Bequaert & Clench, 1934c fig. 13). In the following whorls, these spiral lines become more numerous and somewhat wavy, suggesting the surface had been evenly and shallowly combed. Beginning at 2½ whorls, subtle prosocline, more sparse growth wrinkles compete with the vertical lines; these may impact the suture directly or arcuately. There is little reduction in the intensity of this engraved pattern below the periphery, although there is a slight reduction in caliber. In the last half of the last whorl, the rhomboid pattern may essentially disappear, leaving the growth wrinkles to dominate. Throughout, the shell characteristically remains remarkably smooth and shiny. A subcarina is present in the early whorls, but this disappears in the fifth whorl.

SOFT ANATOMY. Alcohol-preserved specimens available 12/dissected 4. Cameroon: MRAC 3/3, UHZI 1/0; ZMB 7/0; ZMUC 1/1.

Body colour of preserved specimens, including the head and anterior edge of the mantle, is pale-cream fuscous. Dorsally, there is a diffuse grey wash that shades darker anteriorly. A 1–2 mm wide dark gray band with diffuse borders, appears immediately behind the ommatophores and extends posteriorly along the middorsal neck to the edge of the mantle. Surface of body reticulate-microtuberculate. Foot without structural elaborations.

The most prominent feature of the genital system (Fig. 11) is the massive, muscular basal female conduit that seems to be an ill defined fusion of vagina (V), spermathecal duct (SD) and free oviduct (FO). Sessile to this, obliterating the penio-vaginal angle, is the contrastingly short, broad penis sheath (PS). Crowded together and projecting from the apical collar of the PS are the long apical vas deferens (AVD) and the very short penial retractor (PR). In fact, this latter is so short that only its insertion on the broad right columellar retractor (RCR) may be seen. Like that of *L. petitia* and *Callistoplepa barriana*, it inserts far posterior on the RCR (Fig. 2). The tripartite AVD starts as a slender tube, but soon enlarges to form the thick-walled ejaculatory duct. This in turn narrows and then once again enlarges into a thin-walled conduit (possibly a secondary seminal vesicle) before fusing with the FO to form the spermoviduct. When the PS is cut longitudinally, it is found to be extremely thin and attached basally only about half way down on the stubby, dome-shaped penis (P). Both the inner surface of the PS and the outer surface of the P are smooth and shiny, facilitating extroversion. In this aspect, the PR is seen to hood over the apical P and, about one-quarter the way down, blend with the substance of the thick-walled P. When the PR is split longitudinally and its muscle bands spread apart (Fig. 12), the basal vas deferens (BVD) is seen within, discreet and without muscle or connective tissue attachment. Vertically cutting the penial wall reveals a conspicuous, pendulous, vertically oriented pilaster (PIL) whose thick transverse-diagonally textured brownish, glandular epithelium is continuous with the inner wall of the penis. Ventrolaterally on the PIL is a 1 mm vertical eccentric apertural slit. This leads internally to a funnel shaped penial sacculus, which joins the extension of the BVD in a dense mass of connective tissue. It is clear at this point that the PIL has been formed by a permanent partial eversion of the P. In the process, the basal-most BVD, with its diagonal anchoring muscle strands, forms the axial conduit of the PIL (Fig. 13). During extroversion, to form the intromittent organ, the PIL would take the lead, followed by the basal P, and finally the PS, which would contain the BVD, PR, and a portion of the RCR. Both PR and RCR would be involved in the introversion process.

The alignment of the V, SD and FO insures that the intromittent organ will be channeled directly to the SD. This has been accomplished not only by a large knob of tissue eccentrically blocking the narrow lumen of the FO, but also by a massive buildup of muscular tissue surrounding the large lumen of the basal SD. These modifications, in turn, tend to wedge the SD between P and FO (Fig. 11). Internally, there is a sharp division between the thick-walled, heavily muscular V, with its many narrow, tightly compressed, vertical plicae, and the thick-walled basal half of the SD (functionally an extension of the V), with its several bold, deep, coarse vertical plicae. Cutting across these latter plicae are transverse vermiculate rugae that produce a grossly serrate texture on the crests of the plicae. This rough texture seems to complement that of the P and PIL. All these structures obviate the necessity of a distinct muscular vaginal retentor found in many species of Achatininae. The apical SD is thin-walled, as is the clavate spermatheca (S). The apical saccular FO probably serves to hold the large egg immediately before expulsion; basally, however, it is thick-walled, with a narrow lumen. An 'elbow' tends to form at the junction of the two parts. The lower portion and the collar-like thick-walled V doubtless serve as an ovijector.

Three of the four dissected specimens had the uterus and oviduct crowded with 4, 6 or 8 relatively large, off-white hard-shelled eggs, measuring 4.3×3.7 – 5.1×4.4 mm. Their long dimension is ca. 15% of the adult shell length, which is in strong contrast, for example, to that relationship in *Achatina achatina* at ca. 5%. All gravid specimens were collected September–November, just before the long dry season, and because of the demands of producing eggs, they manifested considerable emaciation, especially in the digestive system. Such observations raise the unanswered question of longevity in this small species. In a single specimen, six ovotestis acini were found under the columellar surface of the apical lobe of the digestive gland. The talon is extraordinarily long and slender and without a basal enlargement.

TYPE MATERIAL. The type of Morlet's *Achatina mollicella*, collected by Vignon, has never been illustrated and its very existence has been uncertain. It is not in the Morelet material in the Paris, Geneva or Tervuren collections. Fulton (1920) reported that he had purchased the Morelet land and freshwater shells in 1892, including 'all the types', but that in transit between Dijon and London many of the fragile specimens, including some types, were broken. The BMNH accession book under date 2 April 1893 confirms this information. It lists the accessioned types (pp. 230–254, 2049 entries) including a single entry indicating that there were only two specimens: '93.2.4.119–120 *Achatina mollicella*, Gabon'. However, neither of these two syntypes have the length-width measurements of '18 × 12 mm' given by Morelet (1860) for an individual 6 whorl specimen. Under the circumstances, it is most likely that the 6 whorl syntype is the one Morelet had in hand. Further, there clearly is an error in his reported measurements because in the 35 specimens examined in the present study, the shell width averages 52% of shell length, not 67% as would be the case if Morelet's measurements were correct. For these reasons, the larger syntype BMNH no.93.2.4.119 is here selected as the lectotype (Figs. 27, 28; Table 3) and BMNH no.93.2.4.120 selected as paralectotype. Morelet's incorrect measurements have contributed greatly to the confused synonyms of his valid species and Jousseaume's valid species *Petitita petitia*.

The lectotype and 10 paralectotypes of von Martens' junior subjective synonym *Achatina pulchella* are in Berlin (ZMB; Kilius, 1992), type locality Bonjongo, Cameroon. Additional single specimens here designated as paralectotypes have been found and labeled in Stockholm (SMNH no.4282) and Tervuren (MRAC no.5315). The holotype (monotypy) of Sowerby's junior subjective synonym and junior primary homonym *Achatina smithi* no.89.11.18.1 is in London (BMNH), type locality 'Calabar, Africa'. The holotype of Bequaert & Clench's *Leptocala mollicella zenkeri* (1934c fig. 6) plus two paratypes (their fig. 7 and one unfigured) are in Berlin (ZMB; Kilius, 1992). A third paratype is at Harvard (MCZ) under No. 98687, which was identified by the distinctive mark at the junction of the ultimate and penultimate whorls (cf. their fig. 5). All these were from Yaoundé. A fourth paratype, unfigured but listed on their page 119 is from Bitye (BMNH, no.1908.6.3.2; Table 3).

TYPE LOCALITY. Morelet (1860) lists it as, 'Habitat, rara, in sylvis Guinea.' His two syntypes in BMNH were more specifically labeled 'Gabon,' which is included in the early broad generic geographic term 'Guinea.'

DISTRIBUTION. Sowerby (1890) described *Achatina barriana*

Table 3 *L. mollicella* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Width	% whorl	% LW/L	% W/L	
6¼	39.8	18.7	17.5	9.3	27.7	70	47	Bitya (BMNH) Para <i>L. m. zenkeri</i> 1908.6.3.2
6½	37.5	17.7	17.3	8.9	26.5	71	47	Ebalowa (UMMZ)
6¼	35.8	17.5	18.4	8.7	26.5	74	49	Yaoundé (UMMZ)
6½	33.3	17.3	15.9	10.3	23.4	70	52	Olounou (MRAC) 796.850
6	30.5	16.1	15.6	8.2	22.3	73	53	Kribi (MRAC) 795.638†
6	30.0	14.8	15.0	7.5	21.4	71	50	Calabar (BMNH) Holo <i>A. smithi</i>
6	26.7	13.4	12.8	6.2	18.9	71	50	Gabon (BMNH) Lect. <i>A. mollicella</i> *
6	26.6	14.0	13.6	6.9	19.1	72	53	93.2.4.119 Bonjongo (MRAC) 5315 PLec A.
5½	23.6	13.1	12.4	6.6	17.3	73	55	<i>pulchella</i> Gabon (BMNH) PLec <i>A. mollicella</i> 93.2.4.120
4¾	16.6	10.4	9.1	5.0	12.2	73	63	Nyong (ZMUC)†

Total specimens examined: 35. Sources: BMNH, IRSN, MNHN, MRAC, NHMW, NMW, SMNH, UMMZ, ZMUC.

and *A. smithi* (= *L. mollicella*) at the same time and indicated for both that the locality was 'Calabar, Africa?' (4° 57' N, 8° 19' E). Both specimens were from the Cuming collection, in which a number of other locality records from time to time have been questioned or proven incorrect. J.C. Reid of the University of Calabar has collected near Calabar what is now confirmed as *Callistoplepa barriana*, but so far no *L. mollicella*. It is altogether possible that this latter species eventually will be found in Nigeria because Mbonge, Cameroon, a known endemic locality for this species, is only ca. 70 km to the southeast in a similar environment. Ortiz & Ortiz (1959:26) have reported the western-most records for this species from four localities on Fernando Póo Island (= Macias Nguema Biyogo) of Equatorial Guinea 3° 30' N, 8° 40' E. Seventeen locality records on the continent cluster in the northwestern corner of Cameroon, with the extremes being Mbonge 4° 33' N, 9° 05' E in the North, Molobo 4° 01' N, 14° 19' E in the East, and Efulen 2° 42' N, 10° 30' E in the South. Vignon through Ancy (1888:70) records this species as being very rare in the forests of Gabon. It probably is not found south of the Ogooué River.

In the specimens examined, there was a high direct correla-

tion between greater shell size and distance from the sea-coast, e.g. the largest specimen seen in this study is from Bitya on the river Dja, ca. 260 km from the coast 3° 01' N, 12° 22' E (BMNH no.1908.6.3.2; Table 3).

Leptocala petitia (Jousseaume, 1884)

Figs. 29, 30

Petitia petitia

Jousseaume, 1884:172, pl. 4, fig. 4a, holotype, monotypy (*non* Chitty, 1857); Bequaert, 1950:138.

Achatina (Leptocala) mollicella petitia

Pilsbry, 1904:73, pl. 34, fig. 15 (ex Jousseaume, 1884); Bequaert, 1950:138, pl. 58, fig. 4.

Leptocala mollicella petitia

Bequaert & Clench, 1934b:273.

SHELL. Shell ovate-elongate, thin but not fragile; last whorl shiny, upper whorls less so. Whorls 6½–7, moderately convex. Spire slender conic; apex narrowly obtuse; sutures fine, almost without irregularities. Last whorl expanding proportionately to upper whorls, 70% of shell length (n=7); fourth and fifth whorls subcarinate. Aperture elongate-oval, milky within. Columella short, straight, transversely to obliquely truncate. Outer lip thin, arcuate, joining the periphery at an acute angle. Parietal callus minutely granular, shiny, concolorous.

Shell ground colour is pale corneous. At the junction of the fifth and sixth whorls, diffuse yellow-brown stripes (0.3–0.5 mm wide) alternate with wide ground colour bands (0.5–0.7 mm); these are approximately the same width on the early whorls, but become slightly or much narrower, more distinct and closer together on the last whorl, or nearly disappear; they may be variously straight, diagonal or rippled.

The last quarter of the first whorl has nearly imperceptible surface irregularities that originate close to the suture, where they evolve into a series of closely packed crescentic lines. They quickly multiply axially into five or six horizontal series of short crescentic lines. These gradually fuse vertically to form very narrow, crowded, thread-like, prosocline welts. A fairly conspicuous diagonal line, near mid third whorl, marks the end of the nepionic whorls. Near there, the welts become superficially engraved with a vertically oriented, exceedingly fine vermiculate-granulate sculpture, which is reminiscent of the much coarser sculpture of *Achatina (Tripachatina) vignoniana* Morelet, 1874. Gradually, the welts diminish and the more sparse growth lines emerge, leaving the rash-like microscopic sculpture to dominate. This is best seen in subdued light at a low angle. The sculpture may diminish and become more sparse between the third and fourth whorls, as it does in the holotype, or it may continue at essentially the same caliber until the fourth or fifth whorl. At a certain point in the diminution, and if the light intensity is properly adjusted, ghost-like, engraved spiral lines, here and there, spaced as in *L. mollicella*, can be distinguished, especially below the periphery, where the sculpture is somewhat reduced in calibre. The sculpture may extensively obscure these spiral lines and all but traces of a rhomboid pattern, or it may become so sparse on the lower whorls as to allow the sharp spiral lines to dominate. It is almost as if the vermiculate-granulate sculpture were superimposed upon the typical sculpture of *L. mollicella* in a variably decreasing intensity from apex to base. As a result, the surface of the

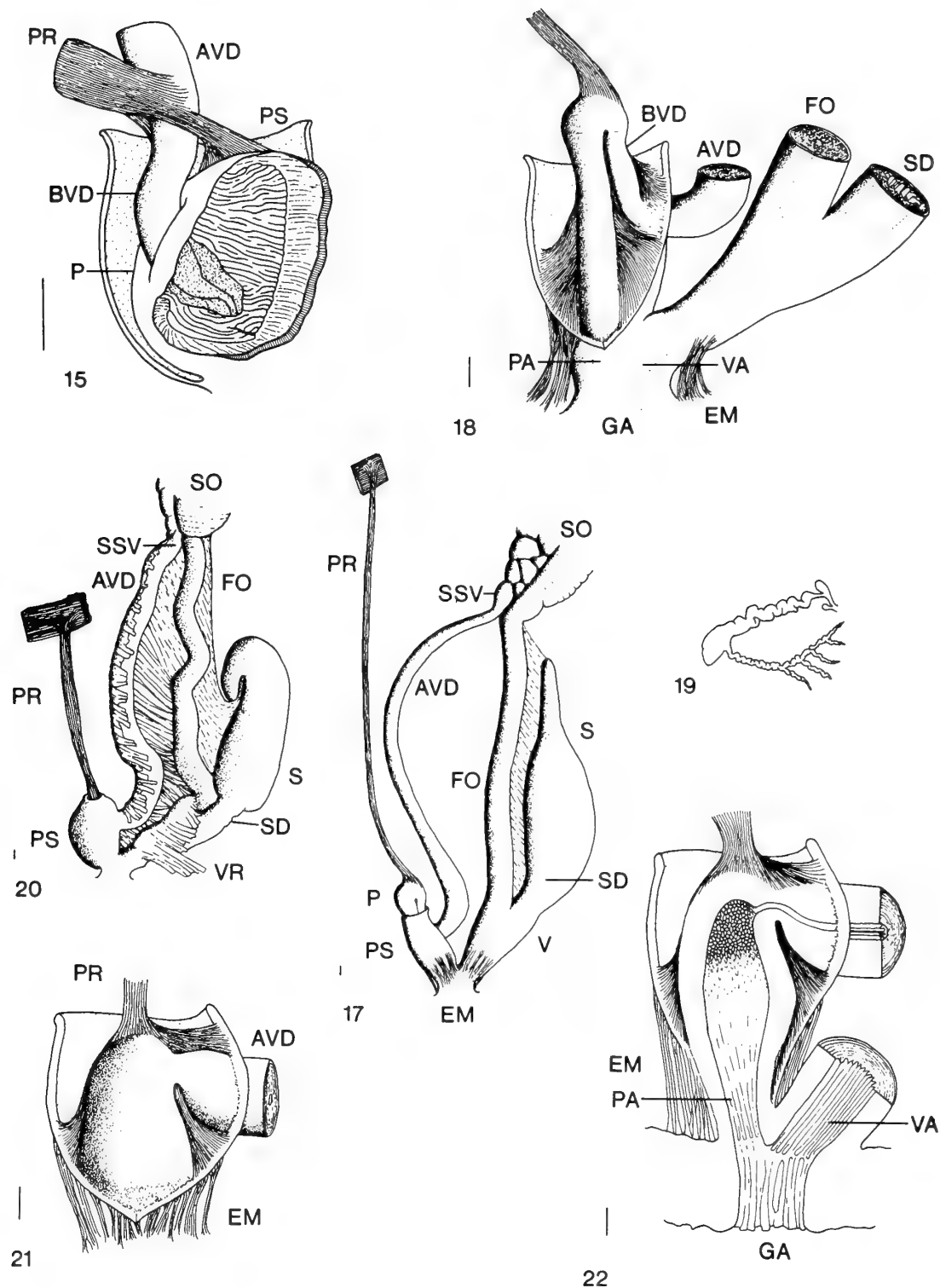


Fig. 15 *L. petitia*, penis sheath and penial wall cut diagonally in right ventrolateral view and spread to expose the pilaster. The cutaway shows the basal vas deferens joining the aperture of the pilaster (MRAC no. 214.044 & 212.583).

Fig. 17 *Bequaertina pintoï*, basal genital structures (NM).

Fig. 18 *B. pintoï*, penis sheath cut and spread laterally. Conduits transected. Most of the obscuring basal eversion muscle bands have been removed.

Fig. 19 *B. pintoï*, hermaphroditic duct system.

Fig. 20 *Bequaertina graueri*, basal genital structures (MRAC no. 610.342 & 610.303).

Fig. 21 *B. graueri*, penis sheath cut and spread.

Fig. 22 *B. graueri*, frontal plane through basal male and female conduits. Bar scale = ~ 1 mm. A.R.M. del.

shell has less luster than in this latter species. This peculiar microscopic sculpture on the upper whorls is determinative.

SOFT ANATOMY. Alcohol preserved specimens available 2/dissected 2. Congo Republic: MRAC 1/1; Zaire: MRAC 1/1. These apparently are the only such specimens extant. Both had small body masses and were withdrawn far into their thin shells because they were collected during the dry season and were inadequately drowned before preservation. However, most of the soft parts were successfully extracted with only minimal damage to one shell.

Body colour and texture as in *L. mollicella*.

Upon exposing the reproductive tract (Fig. 14), the most noticeable anatomical feature is that both the unusual hull-shaped penis (P) and the large basal vas deferens (BVD) show through the thin, nearly transparent, but substantial, penis sheath (PS). Typical of the Callistoplepinae, the PS also enshrouds the very short penial retractor (PR). As in *L. mollicella* and *Callistoplepa barriana*, this latter inserts far posterior on the large right columellar retractor (RCR). Also conspicuous is the apparently inordinately long bipartite apical vas deferens (AVD), with a nearly evenly broad muscular basal portion and a thin-walled, somewhat undulant apical portion. When the PS was cut vertically and the edges pulled laterally, it was found to extend essentially to the base of the P. In the first dissected specimen, from Lukula, Zaire, the exposed, large BVD appeared out of proportion and excessively deeply wedged into the ventral surface of the P. Similarly, the navicular P, with its diagonal left ventrolateral orientation, seemed enigmatically distorted. But the second specimen, from Kayes, Congo Republic, ca. 180 km to the north, had almost identical proportions and alignment, thus essentially removing the suspicion that there had been excessive distortion. The relatively thin penial wall of the first specimen was cut along a midventral, vertical line. Immediately below the surface was a large, obstructing mass of penial wall tissue whose angulate orientation could not safely be explored. Consequently, in the second specimen, a diagonal cut was made along the long axis of the oblong P. This revealed in right ventrolateral aspect a comparatively huge, somewhat compressed potato-shaped pilaster (PIL) attached diagonally along nearly its full length ventrolaterally on the inner basal penial wall, parallel to the adjacent crowded BVD (Fig. 15). In essence, the wall of the basal half of the P was hardly more than a thin, tight-fitting cover for the PIL. The surface of the PIL and the inner wall of the P, similar to that of *L. mollicella*, was covered with transverse, diagonal, anastomosing rugae. Irregularities in the rugae revealed a small basal aperture. Cutting basally into the 2.6 mm PIL exposed the short basal-most BVD narrowing rapidly through dense connective tissue to connect with this aperture. Apically, the PIL is a solid mass of penial wall tissue. Collectively, the relationships in these structures are reminiscent of those in *C. shuttleworthi*, particularly with respect to the exposed BVD pushing ventrally far down into the partially evaginated P (Figs. 4, 5).

In this species the basal female conduit, externally and internally, is much less gross than in *L. mollicella*. The vagina (V) is a distinguishable, more slender portion of the conduit. Similarly, the basal spermathecal duct (SD) is less muscular and tends less to interject itself between PS and the free oviduct (FO). However, the FO, muscular at the base and thin-walled apically, is less robust yet comparatively more prominent in this species. Although shown spread apart in

Fig. 14 for clarity, the FO and basal SD are actually held tightly together by many small, short muscle bands, probably providing support for the SD at termination of copulation. In that natural position, the clavate spermatheca (S) is attached by thin muscle bands and connective tissue to the uterine portion of the spermoviduct, well above the junction of AVD and FO. The eggs are not known but are probably on a par with those of *L. mollicella*.

TYPE MATERIAL. The holotype (monotypy) (Figs. 29, 30; Table 4) in the Jousseume collection in Paris (MNHN) was collected by L. Petit.

TYPE LOCALITY. At the mouth of the River N'toc, which disappears in the Mayumba Lagoon, Gabon 3° 25' S, 10° 39' E.

DISTRIBUTION. Gabon: type locality. Congo Republic: Sibiti 3° 41' S, 13° 21' E (SMNH), Kola 4° 03' S 11° 44' E (MRAC), Kayes 4° 26' S, 11° 23' E (MRAC). Zaire: Lukula 5° 21' S, 13° 02' E (MRAC). All known localities are south of the Ogooué River of Gabon. This species will probably be found in Cabinda, Angola.

REMARKS. In addition to the holotype in Paris (MNHN), there are only six known specimens of this species, five in Tervuren (MRAC), collected by Darteville, and a single specimen in Stockholm (SMNH). The explanation for its apparent rarity probably rests in the fact that there has been much less professional collecting in south coastal Gabon and the Congo Republic than in Cameroon, where *L. mollicella* is not a rarity. In this limited number of specimens extant, there is a north to south gradient of more intense vermiculate-granulate sculpture and reduced rhomboid pattern. If the substantive differences in the soft anatomies had not been known, this taxon might well have been assumed to be no

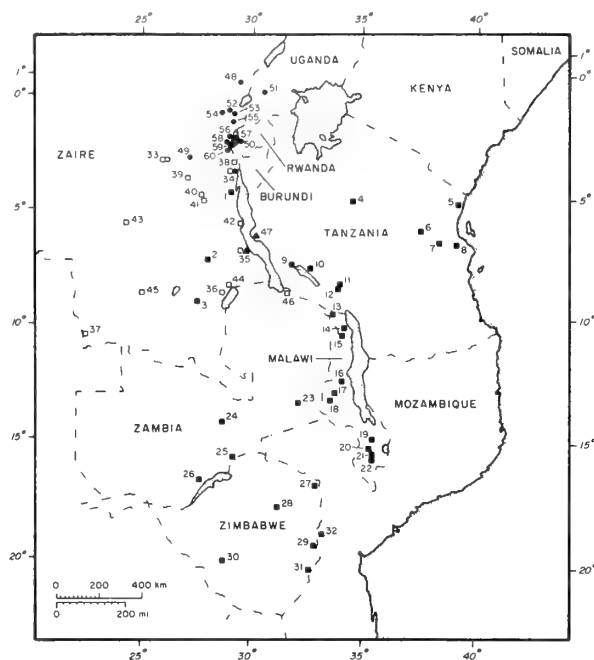


Fig. 16 Distribution of *Bequaertina*. ○ = *Bequaertina fraterculus*, ● = *B. graueri*, □ = *B. pellucida*, ■ = *B. pintoi*, ▲ = *B. marteli*. Where possible, all localities were checked with the volumes of the U.S. Board on Geographic Names.

Table 4 *L. petitii* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Width	% whorl	% LW/L	% W/L	
7	32.5	14.8	14.3	7.5	21.5	66	45	N ^o toc (MNHN) Holo *
6½	30.9	14.2	14.5	7.1	21.4	69	46	Sibiti (SMNH)
6¼	30.8	14.8	13.9	7.2	21.3	69	48	Lukula (MRAC) 212.583 [†]
6½	29.0	13.7	14.0	6.5	20.1	69	47	Kola (MRAC) 196.340
6	28.6	14.6	14.5	7.1	20.5	72	51	Kola (MRAC) 196.341
6	23.9	12.3	11.6	6.0	16.4	69	51	Kayes (MRAC) 214.004 [†]
5	20.8	13.3	11.8	6.3	15.1	72	64	Kola (MRAC) 791.389

Total specimens examined: 7. Sources: MNHN, MRAC, SMNH.

more than a subspecies of *L. mollicella*, as Bequaert & Clench concluded (1934b:273). This case is reminiscent of the conchologically very similar but anatomically contrasting *Achatina reticulata* Pfeiffer, 1845 and *A. albopicta* E.A. Smith, 1878 (Mead, 1950:232).

Jousseume's illustration of the holotype is misleading because the artist has shown the apex acuminate; actually, the first and second whorls are noticeably larger, producing a narrowly obtuse apex.

Apparently neither Leonardo Fea (Germain, 1916) nor Captain Vignon (Ancey, 1888) went far enough south in Gabon to encounter true *L. petitii*.

ACHATININAE

Bequaertina new genus

Thin, fragile, anomphalous, medium to large, ovate to ovate-elongate shells, 40–80 mm in length. Spire tends to be mammillate, apex obtuse. Aperture large, columella long and slender, squarely or obliquely truncated. Whorls 6–6½, rarely 7; second and third nepionic whorls sculptured; last whorl ventricose, ca. 80% of shell length. Sculpture may be variously cancellate-granulate, lirate, malleate or nearly smooth. Surface of shell lusterless; its abrasion reveals a brilliant inner periostracal layer. An occasional specimen may show in the periostracum of the lower whorls limited areas of an extremely fine decussate micromesh, commonly seen in a wide variety of achatinids.

The generic characters in the soft anatomy are based on features that are shared by the two available species – *B. pinto* (Bourguignat, 1889) and *B. graueri* (Thiele, 1911). Because of the similarity in the basic anatomical pattern in these two species, and because, on the basis of shell characters, each of the species represents a different dichotomous group, it is felt that the following anatomical characters will prove to be valid for the genus.

The most prominent features of the genital system are the long free oviduct, the apical vas deferens and the large,

elongate sacculate spermatheca – all held in close juxtaposition by a distinct fascia. In contrast, the penis and penis sheath are inconspicuous. The penis sheath enshrouds a short basal portion of the long vas deferens. Without exception in 26 dissected specimens, the penial retractor inserts on or near the diaphragm where the latter joins the mantle and the body wall of the neck region. At the origin of the penial retractor, muscle fibrils pass snugly over the apical penis and then fan out into a network that covers the basal vas deferens and the inner wall of the penis sheath, except for a limited smooth, shiny zone on the approximately upper half of the left side. Below this, the fibrils infuse intimately with the tissues of the basal penis and penis sheath to create an ill defined section of the male conduit that contains the penial atrium. This atrium connects the lumen of the penis with the genital atrium. At this level, abundant hypertrophied eversion muscle bands obscure the genital atrium and its junction with the male and female conduits. There is no pilaster or verge.

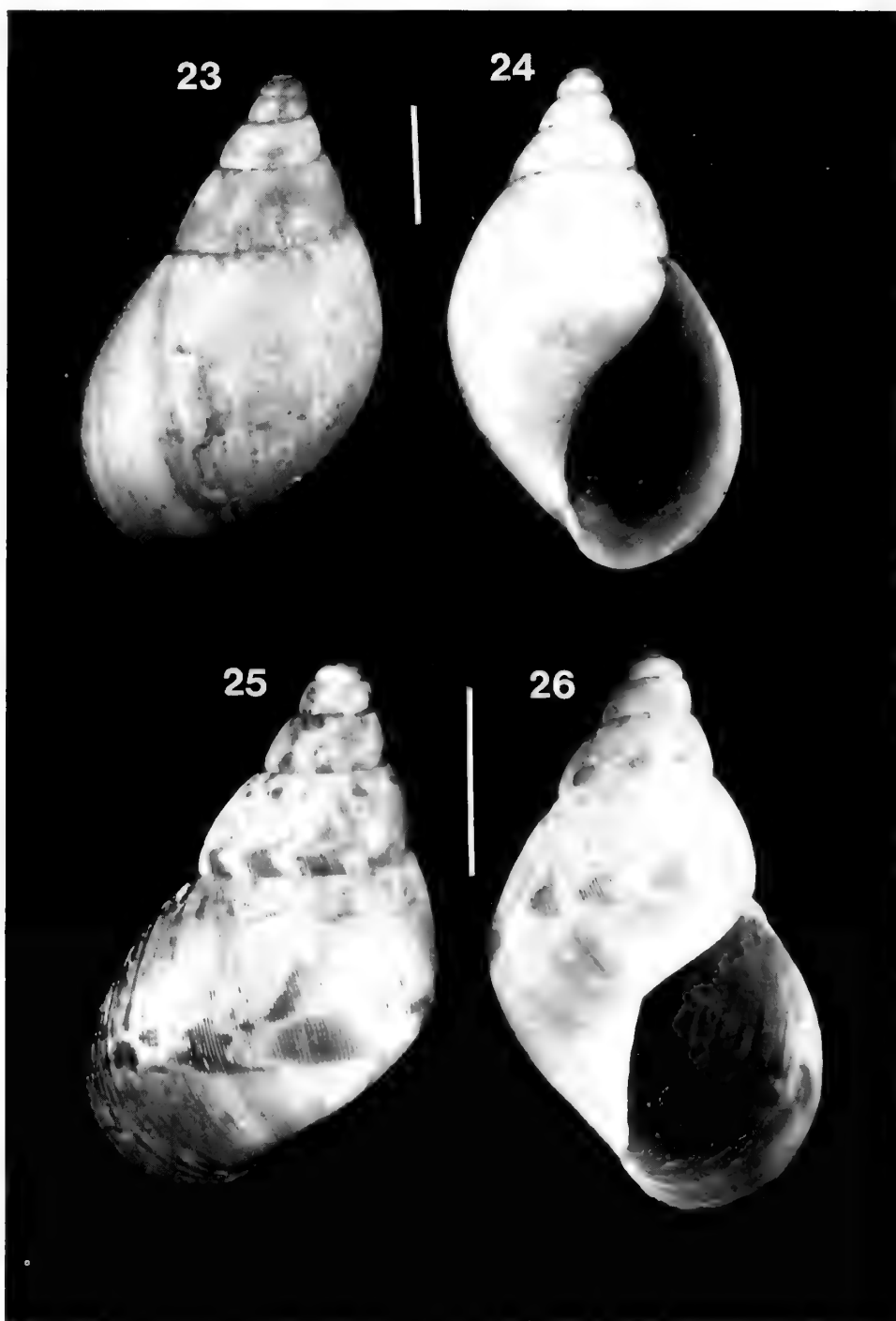
The spermathecal duct is much shorter than the spermatheca and often sessile on the vagina. This significantly places the spermatheca in a basal position with its usually attenuated apex stretching to its connection by fascia to the junction of the free oviduct and the apical vas deferens, well below the spermoviduct. The hermaphroditic duct has in its midsection an enlarged glandular structure of unknown function. The ductules to the five hermaphroditic acini are inordinately gross and highly convoluted.

The eggs are covered with a hard calcareous shell and are proportionately larger than those of *Achatina*, i.e. on a par with those of *Tholachatina* (*sensu* Bequaert, 1950). There is no evidence of ovoviviparity.

The anterior aorta is on the floor of the diaphragm and passes ventrally through the diaphragm to the sagittal myoseptum in the haemocoel. The second largest vein in the lung drains the region near the extreme left mantle and joins the primary vein near the apex of the kidney. The large last whorl of the shell allows for a highly vascularized left side of the lung. The secondary ureter is completely closed. The rachidian tooth of the radula is either slender and questionably functional or broad and about half the size of the adjacent laterals. The jaw is narrow and broadly arcuate, with many slender vertical ribs irregularly distributed.

Six specimens of *B. pellucida* (Putzeys, 1898) and one of *B. marteli* (Dautzenberg, 1901), as well as several of *Achatina craveni*, have been found with a single, almost perfectly circular hole, 0.6–4.0 mm in diameter, cut usually in the dorsal part of the last whorl. These are thought to be caused by bird pecks (Meredith, 1983a:25).

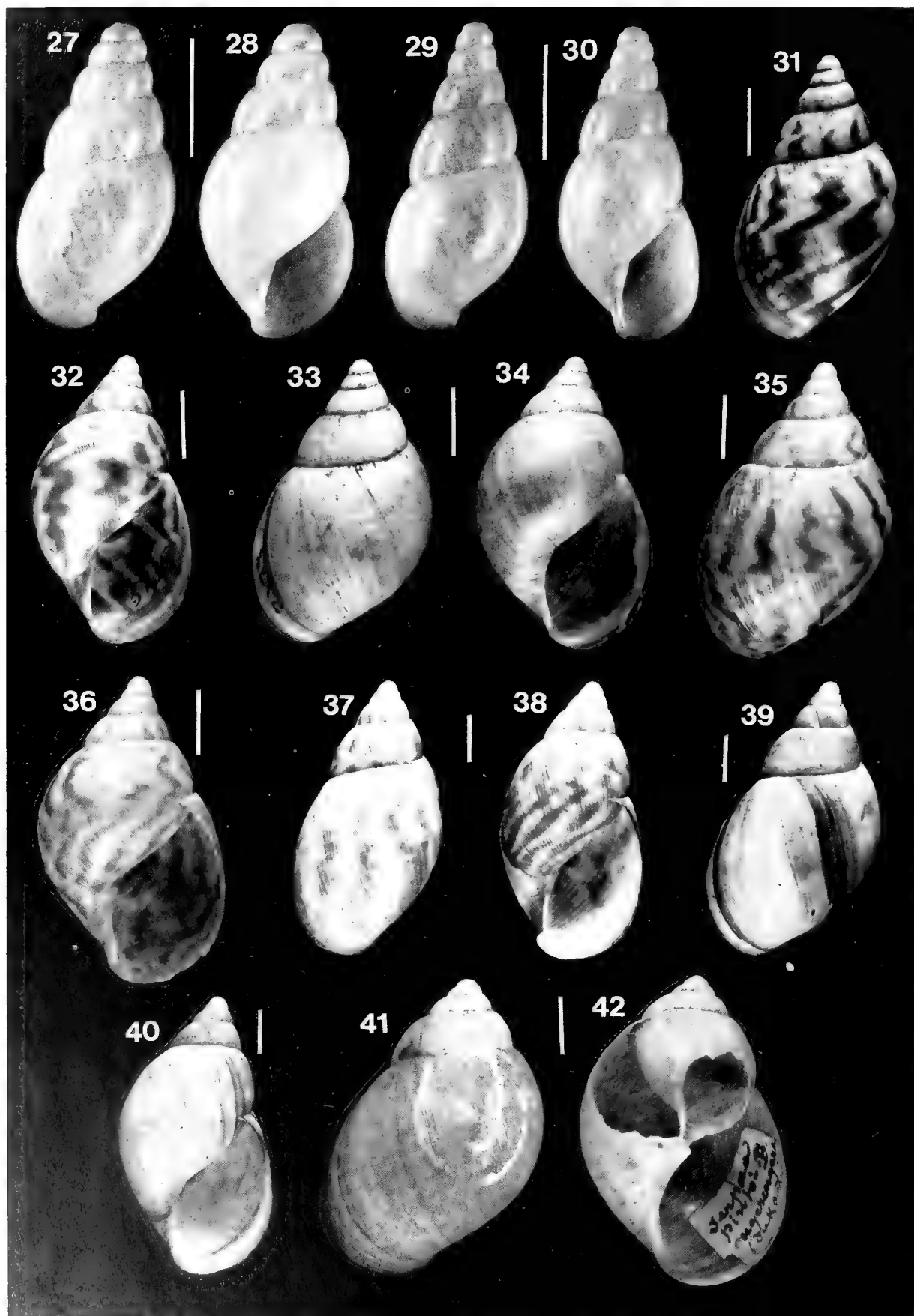
The five species in this genus were placed in the genus *Callistoplepa* on the basis of similar shell characters: thin shell, large aperture and a tendency to form a mammillate spire (Pilsbry 1919, Bequaert & Clench 1934c). But as shown in the Key to Subfamilies, a study of the internal anatomies revealed major differences. *Bequaertina* reflects strongest phylogenetic affinities to subgenus *Achatina* (*sensu* Bequaert, 1950), particularly with respect to the configuration of the basal male conduit and to the fact that the spermatheca is attached to the adjacent free oviduct and apical vas deferens rather than to the spermoviduct. In *Bequaertina*, the apical penis is free from the apical penis sheath and therefore can evert independently, with the sheath following seriatim at extroversion, whereas in subgenus *Achatina* the penis is completely enmeshed in a dense network of muscle fibrils and connective tissue that requires the penis and the sheath to

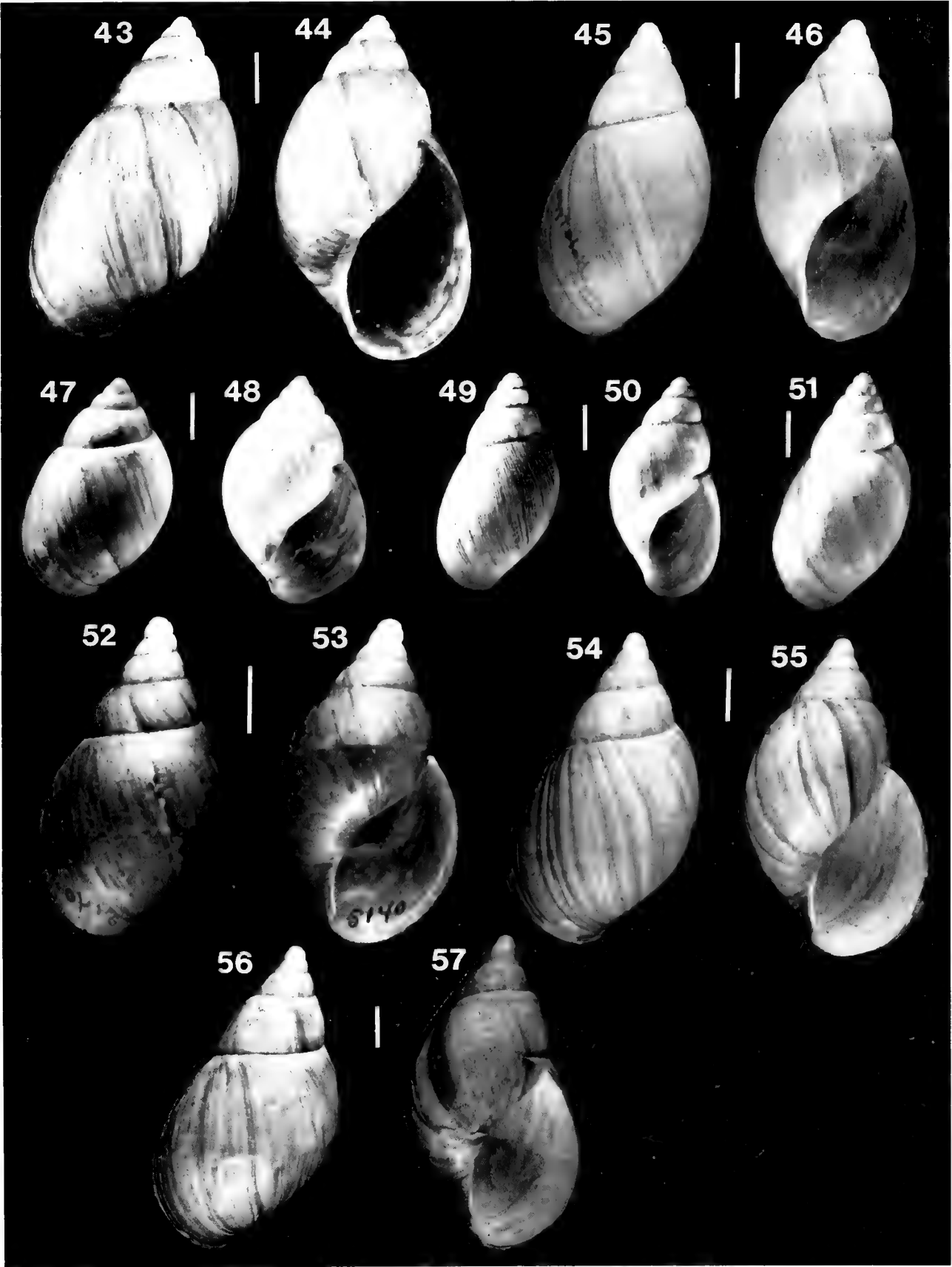


Figs 23, 24 *Callistoplepa barriana* (Sowerby, 1890); lectotype *Achatina barriana* BMNH no. 1889.11.19.2. **25, 26** *C. shuttleworthi* (Pfeiffer, 1856); lectotype *Achatina shuttleworthi* BMNH. Bar scale = ~ 10 mm.

Figs 27, 28 *Leptocala mollicella* (Morelet, 1860); lectotype *Achatina mollicella* BMNH no. 93.2.4.119. **29, 30** *L. petiti* (Jousseaume, 1884); holotype *Petitia petiti* MNHN. **31, 32** *Bequertina pellucida* (Putzeys, 1898); lectotype *Ganomidos pellucidus* MRAC no. 5135. **33, 34** *B. pellucida*; paralectotype *G. pellucidus* (unicolorous) MRAC no. 5136. **35, 36** *B. pellucida*; lectotype *Serpaea foai* Germain, 1905 MNHN. **37, 38** *B. marteli* (Dautzenberg, 1901); lectotype *Achatina marteli* IRSN. **39, 40** *B. marteli*; lectotype *A. marteli pallescens* (Dautzenberg, 1901) IRSN. **41, 42** *B. pinto* (Bourguignat, 1889); holotype, *Serpaea pinto* MNHN. Bar scale = ~ 10 mm.

Figs 43, 44 *B. pinto*; lectotype *Achatina fragilis* Smith, 1899 BMNH no. 97.12.31.9. **45, 46** *B. pinto*; holotype, *Callistoplepa thielei*, Bequaert & Clench, 1934c ZMB no. 53177. **47, 48** *B. pinto*; BMNH no. 1885.5.25.47. **49, 50** *B. pinto*; BMNH MacAndrew (1563). **51** *B. pinto*; BMNH no. 1907.7.25.3. **52, 53** *B. fraterculus* (Dupuis & Putzeys, 1900); lectotype *Ganomidos fraterculus* MRAC no. 5140. **54, 55** *B. graueri* (Thiele, 1911); lectotype *Achatina graueri* ZMB no. 101935. **56, 57** *B. graueri*; lectotype *Callistoplepa babaulti*, Germain, 1936 MNHN. Bar scale = ~ 10 mm.





evert together as a unit, forming a quite different intromittent organ. The very shell characters that seemed to link these five species with *Callistoplepa* now are seen conchologically to distinguish the more primitive genus *Bequaertina* from *Achatina* s.s.

On the basis of somewhat overlapping shell characters, available distributional records, and the limited anatomical evidence, the species of *Bequaertina* break into two groups: (1) the malleate, mammillate *B. fraterculus* (Dupuis & Putzeys, 1900) and *B. graueri*, and (2) the cancellate *B. pellucida*, *B. marteli* and *B. pintoii*. *B. pellucida* of southeast Zaire, close to what is believed to be its ancestral home, is plesiomorphic within the group and stands between an ancestral achatinid stock of the Zaire Basin and *Achatina* s.s., which today is largely restricted to that basin. A branch of the ancestral stock moved north and northeast to give rise to the apomorphic *B. fraterculus* and *B. graueri*. A more conservative second branch moved east to give rise to *B. pellucida* and *B. marteli*. This second branch continued further east and then into a strong north-south axis to give rise to the closely related *B. pintoii*. The known distribution of the genus (Fig. 16) embraces a vast area of the Rift Valley – Lake Region and the Lualaba branch of the Zaire River in central, eastern and southeastern Africa. Greater field collecting will probably extend the limited distributions of *B. fraterculus* and *B. marteli*.

Pilsbry & Cockerell (1933), on the erroneous assumption that *Achatina graueri* 'represented an intrusion of a South African type into the Central African region', initially decided to place it in the genus *Cochlitoma*. They softened their stand on the advice of M. Connolly and designated it '*Achatina (Cochlitoma) graueri*'. However, this species cannot possibly be considered congeneric with *Cochlitoma zebra* (Bruguère, 1789), which Pilsbry (1904:xiii, 78) selected as the type species of the genus *Cochlitoma*, because Mead (1992) shows *Achatina zebra* anatomically belongs to subgenus *Tholachatina* of *Archachatina*. Since the present group of five species is not congeneric with the species in either *Callistoplepa* or *Achatina* s.s., and since this group also is not congeneric with *Achatina hortensiae* Morelet, 1866, which Pilsbry (1904:21) selected as the 'type' of *Serpaea*, there is no other available genus-group name. *Ganomidos* cannot be considered because it is a junior subjective synonym of *Callistoplepa*. For these reasons, the generic name *Bequaertina* is proposed. It is named in honour of the late Dr Joseph C. Bequaert, Agassiz Professor of Zoology at Harvard University, who will remain the classical authority not only in the Achatinidae, but also in several families of insects and arachnids that he mastered in his long lifetime. Because *B. graueri* is the largest and most conspicuous of the five species, and because it has departed farthest from what is believed to be the ancestral stock, it is here selected as type species of the genus.

Early in the present study, it became obvious that this group of five species anatomically was not congeneric with *Callistoplepa*. This information was shared with colleagues who considerably referred to this new genus in general terms (van Bruggen, 1978:912, 921, 1988:10; van Bruggen & Meredith, 1984:161). Also, the present author made reference to this new genus in an earlier manuscript as '*Callistoplepa* s.l.' (Mead, 1992).

Key to Species

- 1 Last whorl distinctly granulate above the periphery, or at least in a limited subsutural zone; growth wrinkles conspicuous to dominant 2
- Last whorl faintly granulate, malleate, lirate or smooth except for modest irregular growth wrinkles 4
- 2 Apex broadly obtuse; 6 whorls = > 50 mm; yellowish, ochraceous or olivaceous; gross granulate sculpture; first nepionic whorl 2–3 mm in diameter; second whorl expanding broadly; sculpture of second whorl coarse and either distinctly granular or depressed and poorly defined; transverse measurement at junction of third and fourth whorls is 2½–4 mm; outer lip increasingly arcuate basally; growth wrinkles bold or moderately heavy 3
- Apex subacute to narrowly obtuse; 6 whorls = ~ 40 mm, 7 whorls = 53–60 mm; translucent dull fulvous to dull olivaceous-brown; moderately coarse to fine granulate sculpture; first nepionic whorl 2 mm in diameter; second whorl tends to be slightly constricted, expanding limitedly; sculpture of second whorl finely engraved, delicate; transverse measurement at junction of third and fourth whorls is 2–2½ mm; outer lip evenly arcuate; growth wrinkles thin, of modest calibre. Southeast Zaire, northeast Zambia and west central Tanzania *pellucida*
- 3 Last whorl large, rarely strikingly so; ground colour intense olivaceous-yellow to subdued olivaceous; prominent closely aligned somewhat irregular costate transverse ridges embrace the gross elongate granules with bold vertical emphasis, dominating the spiral lines; strongly contrasting zigzag castaneous flammules usually present, pale unicolorous forms uncommon; first nepionic whorl 2½–3 mm in diameter; sculpture of second whorl coarse, granular, elevated, tightly packed; transverse measurement at junction of third and fourth whorls is 3–4 mm; third whorl deeply and grossly granulate. Middle west and east shores of Lake Tanganyika, Zaire and Tanzania *marteli*
- Last whorl large, often very large to ventricose; ground colour dark olivaceous to pale olivaceous yellow; coarse granulate sculpture above periphery, reduced or absent below periphery (varies within a single whorl); transverse ridges moderate, slender, fairly uniform, in balance with the spiral lines, conspicuous below periphery but obscured by granulate sculpture above periphery; usually unicolorous, but narrow fairly straight light castaneous stripes may be present; first nepionic whorl 2–2½ mm in diameter; sculpture of second whorl coarse, but superficial, vaguely and irregularly impressed, patchy, poorly defined, often worn smooth; transverse measurement at junction of third and fourth whorls is 2½–3 mm; third whorl delicately to moderately granulate. East Africa, almost reaching the Limpopo River in the south (4–20° S, 27–39° E) *pintoii*
- 4 Apex of shell obtuse and noticeably mammillate; shell conspicuously to obscurely malleate; opaque or dark and translucent, uniformly or somewhat variably brown or yellow-brown, banding limited and irregular; coarse growth wrinkles or extremely fine lirae dominate the sculpture, 6 whorls = > 43 mm 5
- Apex of shell subacute to narrowly obtuse, somewhat elevated but not mammillate; shell not malleate; translucent dull fulvous to dull olivaceous-brown, usually with moderately broad castaneous flames and stripes irregularly distributed, but may be pale unicolorous; very fine granulate-cancellate sculpture dominates; 6 whorls = < 43 mm. Southeast Zaire, northeast Zambia and west central Tanzania *pellucida*
- 5 Shell large (6¼ whorls = 60–80 mm), thin but substantial, essentially opaque; usually conspicuously malleate; not carinate; growth wrinkles prominent, rather regular; lirae of fifth whorl distinctly transacted by spiral striae; unicolorous or

Table 5 Locality records – *Bequaertina*. Numbers in the first column correspond to the locality numbers in Figure 16. Sources of specimen information are shown in the last column.

1. Lake Tanganyika, 1800–2000m	4° 30' S, 29° 00' E	NHMH [†]
2. Kiambi	7° 20' S, 28° 01' E	Dautz. & Germ., 1914
3. Sampwe (<i>non</i> 'Sangue')	9° 20' S, 27° 26' E	Dautz. & Germ., 1914
4. Ibahi, Ugogo (=Ougogo) Riv.	5° 04' S, 34° 04' E	Ancey, 1902
5. Mbwe (=Mbwego)	5° 21' S, 38° 58' E	Ancey, 1902
6. Mamboya (=Mambo)	6° 16' S, 37° 06' E	BMNH
7. Morogoro	6° 50' S, 37° 45' E	BMNH
8. Ngerengere, Oukani, Kingoni	7° 03' S, 38° 31' E	Bourg., 1889
9. Ufipa (=Sumbawanga)	8° 00' S, 31° 30' E	Ancey, 1902
10. Rukwa Lk.	8° 00' S, 32° 25' E	BMNH [†]
11. Mbaya, 1700m	8° 45' S, 33° 27' E	BMNH, LNK
12. Utengule	8° 54' S, 33° 20' E	BMNH, MCZ, ZMB, SMF
13. Misuku Hills, Mughoma, 1500m	9° 40' S, 33° 33' E	RMNH [†]
14. Deep Bay (=Chilumba, =Hengwa)	10° 27' S, 34° 16' E	BMNH
15. Nyika Plateau, 6000–7000 ft.	10° 48' S, 33° 48' E	BMNH, IRSN, MCZ et al.
16. Nkoto-Kota	12° 55' S, 34° 18' E	BMNH
17. Nchisi (=Ntchisi) Mt.	13° 20' S, 34° 05' E	HM [†]
18. Chinyama	13° 43' S, 33° 43' E	HM [†]
19. Zomba, Shirwa Lk., Mpita	15° 23' S, 35° 23' E	BMNH, IRSN, RMNH
20. Chiradzulu Mt., Lisau	15° 41' S, 35° 09' E	HM [†]
21. Nyambadwe Hill	15° 48' S, 35° 15' E	NG [†]
22. Soche Mt.	15° 51' S, 35° 01' E	NG [†]
23. Cheri Bridge, Upper Lauangwa	13° 35' S, 31° 30' E	MCZ
24. Broken Hill (=Kabwe)	14° 27' S, 28° 27' E	NMW
25. Kafue Riv., Mumbwa	15° 56' S, 28° 55' E	Beq. & Cl., 1934c
26. Pemba	16° 40' S, 27° 25' E	SAM
27. Mazoe Valley	16° 32' S, 33° 25' E	NMW
28. Salisbury	17° 50' S, 31° 03' E	NM
29. Vumba, Zonwi Bridge, 2500 ft.	19° 07' S, 33° 05' E	NM [†]
30. Bulawayo	20° 09' S, 28° 35' E	RMS, SAM
31. Chirinda, Selinda Mt., 4000 ft.	20° 26' S, 32° 42' E	BMNH, MCZ
32. Macequece, Vila de Manica	18° 56' S, 32° 53' E	BMNH, NMW, SAM
33. Nsendwe, Maniema	2° 57' S, 25° 56' E	BMNH, MRAC
34. Uvira	3° 24' S, 29° 08' E	ZMB
35. Mpala (=Pala)	6° 45' S, 29° 31' E	IRSN
36. Mweru (=Moero) Lk.	9° 00' S, 28° 45' E	BMNH, IRSN
37. Dilolo	10° 42' S, 22° 20' E	SMF
38. Rumonge	3° 11' S, 29° 08' E	MRAC
39. Kapuri (=Piani Kapuri)	3° 34' S, 26° 53' E	BMNH, IRSN, MRAC et al.
40. Luaye	4° 42' S, 27° 23' E	MRAC

variably transversely striated with yellow-brown to dark brown; nepionic whorls densely granulate. Lake Kivu district of Zaire, Rwanda, Uganda *graueri*

- Shell small (6¼ whorls = ~ 50 mm), extremely thin, fragile, translucent; malleations very shallow, often sparse; subcarinate at periphery, producing a bend in the arc of fine prosocline lirae; lirae of fifth whorl not transacted; ground colour dull dark brown-olive with irregular castaneous brush marks that are closely highlighted aperturally with buff; nepionic whorls faintly granulate. Lualaba River, Zaire *fraterculus*

Bequaertina pellucida (Putzeys, 1898)

Figs. 31–36

Ganomidos pellucidus

Putzeys, 1898:84, text fig. 20, 21.

Callistopepla pellucida

Pilsbry, 1905:128, pl. 43, fig. 3, 4; Germain, 1909:90; Pilsbry, 1919:81; Bequaert & Clench, 1934c:114; Haas, 1936:13.

Serpaea foai

Germain, 1905:255; 1908:631.

Achatina foai

Verdcourt, 1966:111; 1983:219.

Callistopepla pellucida

Oliver, 1983:9.

SHELL. Shell ovate-achatiniform to elongate-ovate, extremely thin, very fragile, translucent. Whorls 6–7, rarely 7½; a conspicuous demarcation at or near the end of the third whorl sets off the nepionic whorls. Spire conic, with a narrowly obtuse apex that is slightly elevated; occasionally the second nepionic whorl is somewhat constricted, producing a submamillate profile. Whorls slightly convex, expanding and descending proportionately. Sutures moderately deep

Table 5 continued

41. Kabambare	4° 42' S, 27° 43' E	ZMB
42. Lukuga Riv. mouth	5° 55' S, 29° 12' E	MCZ
43. Gandajika	6° 45' S, 23° 57' E	MRAC
44. Pweto	8° 26' S, 28° 55' E	IRSN
45. Kamina	8° 44' S, 25° 00' E	MRAC
46. Abercorn (=Mbala)	8° 50' S, 31° 22' E	MCZ
47. Kungwe, Sitete (=Nkungwe)	6° 07' S, 29° 48' E	Verdcourt, 1966
48. Beni	0° 30' N, 29° 28' E	IRSN, MRAC
49. Kitembo	2° 53' S, 27° 37' E	MNH
50. Lobengera Mission	2° 03' S, 29° 25' E	MRAC
51. Ibanda	0° 08' S, 30° 30' E	MRAC
52. Loashi Valley	1° 14' S, 28° 45' E	MRAC
53. Burungu, Ruasa	1° 20' S, 29° 02' E	ANSP
54. Nyabukere	1° 29' S, 28° 33' E	MRAC
55. Kirotoche, 1250 m	1° 37' S, 29° 02' E	MRAC
56. Lwiro Riv.	2° 00' S, 28° 52' E	AMNH, FMNH
57. Idjwi (=Kwidschwi, Kwidjwi)	2° 09' S, 29° 04' E	ZMB, MRAC, UMMZ et al.
58. Katana	2° 13' S, 28° 50' E	MRAC
59. Tshibinda	2° 20' S, 28° 45' E	ANSP, MRAC
60. Bukavu	2° 30' S, 28° 52' E	MNH, NMB

[†] = specimens dissected in the present study.

and irregular. Last whorl large, 80% of shell length; range for 5–7½ whorls, 76–84% (n = 52). Aperture oval, faint milky wash within. Columella concolorous, slender, moderately long straight or slightly arcuate and rectangularly to very obliquely truncate. Outer lip extremely thin, evenly arcuate, receding at base in profile. Parietal callus scarcely detectable.

The first two to three whorls are light horn colour. Pale, obscure, castaneous streaks begin to appear in the third or fourth whorl; these characteristically are broader at the suture below, becoming increasingly darker, larger and more irregular on the last whorl. These streaks may be variously vertical, diagonal, angulate, flammulate, interrupted, or reduced to spots and blotches. Ground colour is dull buff to dull olivaceous-fulvous. Of 56 specimens checked precisely for colour, 63% have a definite pattern, 7% are nearly unicolorous, and 30% are unicolorous. There was no correlation between colour pattern and locality.

The first whorl is essentially without sculpture. Minute, faintly engraved crescentic granulations usually appear early in the second whorl; these are formed by nearly equidistant spiral lines and irregular, scalloped transverse lines. The latter become straighter and compressed in the third whorl, producing narrow elongate granulations and irregularly appearing prosocline growth wrinkles that are crenulate at the suture. The sculpture becomes more disperse in the fourth and fifth whorls, producing a dominant, fairly uniform, subquadrate, often welt-like, cancellate-granulate sculpture, which usually fades quickly at the periphery. In the sixth to seventh whorls, this sculpture becomes more and more subdued and diffuse until the increasingly prominent, yet modest, growth wrinkles dominate both above and below the periphery. In the largest specimens of seven whorls the cancellate-granulate sculpture may feebly or strongly return both above and below the periphery. The dull, extremely thin, tenaceous outer periostracal layer wears off in very limited areas, highlighting the sculpture with the exposed glossy inner periostracal layer.

SOFT ANATOMY. No known alcohol preserved specimens.

TYPE MATERIAL. As nearly as can be determined, Putzeys had 14 syntypes of his *Ganomidos pellucidus*, for which he gave a range of shell dimensions (1898). The specimens were collected by P. Dupuis. Putzeys retained a select series of 7 syntypes in his own collection (MRAC no.5132–5138). He did not designate types, but selected the largest specimen (no.5132) for an abapertural view and a small specimen with slender flames (no.5133) for an apertural view in his line drawing illustrations. Regrettably, the larger specimen had been rather badly damaged and mended in nature, and the smaller specimen was excessively small. The second largest syntype in his series (no.5136) is a unicolorous specimen that is representative of only about a quarter of the known specimens (Figs. 33, 34). Hence, the flamed, third largest syntype in his series (no.5135) is here selected the lectotype (Figs. 31, 32; Table 6), with the other syntypes becoming paralectotypes (BMNH 1no.1904.5.18.68, IRSN 5, MRAC 6, NHMW 1).

On the basis of two specimens collected by Edouard Foa during his 1897–98 expedition to the Lake District of Africa, Germain described (1905) and figured (1908) the junior subjective synonym *Serpaea foai* from 'Tanganika est', later corrected to 'les bords du Lac Tanganyika'. Bequaert (1950) placed *Serpaea* in the synonymy of *Achatina*, but apparently

Table 6 *B. pellucida* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl % LW/L	% W/L	
7	60.4	31.4	32.7	19.5	45.9	76	52 Mweru (BMNH)
7½	58.6	32.8	36.0	16.6	46.0	79	56 Kamina (MRAC) 581.196
7	54.5	29.0	30.5	17.0	42.5	78	53 Mweru (BMNH) 1907.11.11.5
7	53.3	30.2	31.2	17.8	42.3	79	57 Mpala (IRSN)
6½	48.0	28.0	29.7	15.8	38.0	79	58 Piani Kapuri (MRAC) 5132 PLec G.p.
6½	46.9	29.6	29.4	16.5	37.5	80	63 Tanganyika (MNH) Lect S. foai *
6¼	45.8	28.0	28.0	16.7	37.0	82	61 Piani Kapuri (IRSN) PLec G.p.
6½	45.0	28.2	26.8	15.5	35.5	79	63 Piani Kapuri (MRAC) 5136 PLec G.p. *
6¼	43.2	24.6	25.5	14.1	33.9	78	57 Piani Kapuri (MRAC) 5135 Lect G.p. *
6¼	40.4	22.6	23.0	13.6	31.7	78	56 Piani Kapuri (MRAC) 5133 PLec G.p.
6	39.0	23.3	24.4	14.1	32.0	82	60 Tanganyika (MNH) PLec S. foai
5¾	35.5	20.0	20.9	12.0	28.4	80	56 PLec G.p. (BMNH) 1904.5.18.68

Total specimens examined: 62. Sources: BMNH, IRSN, MCZ, MNHN, MRAC, NMW, USNM, ZMB.

overlooked Germain's species. Only Verdcourt (1966) has acknowledged the existence of this species, and then only as an East African species unknown to him. A study of the two syntypes in Paris (MNH) confirmed the fact that they are indeed Putzeys' species. His larger, sharply photographed 'seul adulte' specimen (Figs. 35, 36) is here selected as the lectotype of Germain's *Serpaea foai* (Table 6).

Deshayes (1824–37, 1864) described and illustrated a small fossil snail *Agathina pellucida* (= *Achatina pellucida*) from the Paris basin. Lamarck (1838:313) also refers to this species. This very acuminate, slender specimen is possibly a subulinid. It does not enter into homonymy with Putzeys' *G. pellucidus* because the latter was never included in the genus *Achatina*.

TYPE LOCALITY. Forest of Piani Kapuri, Maniema (=Manyema), Zaire 3° 34' S, 26° 53' E.

DISTRIBUTION. Next to *B. pintoï*, this is the most wide spread species in the genus (Fig. 16). The known specific localities delineate essentially the southeastern quarter of Zaire, with Nsendwe, near Kindu-Port-Empain, Maniema region in the northwest; Uvira, Kivu region in the northeast; Mpala, Tanganyika region in the east; Lake Mwero (=Moero), Kantanga region in the southeast; and Dilolo, Lualaba region in the southwest. The only records outside Zaire are (1) in Abercorn (= Mbala) at the southern tip of Lake Tanganyika, Zambia, and (2) on the Tanzanian east shores of this lake, based on Germain's synonym *Serpaea foai* (1905, 1908). Meredith (1983b) and N. Gray (correspondence) failed to find it during extensive collecting in Malawi. The largest and finest specimens extant were collected in the Lake Mwero region (BMNH) and Kamina (MRAC).

REMARKS. This plesiomorphic wide spread species is most closely related to *B. marteli*. Specimens have been found in mixed lots along with *B. marteli* and *Achatina craveni*. The juvenile specimens of all three species are easily confused. Further, the full grown specimens are quite variable in shape, colour, sculpture and pattern, with the not uncommon atypical forms of each species contributing to the difficulty of identification. The young specimen that Grauer collected in the virgin forest 50 km east of Kasongo, Zaire, and identified as *Achatina fulminatrix* von Martens, 1895 by Thiele (1911:205) was examined in Berlin (ZMB) and found to be *B. pellucida*. Extensive series of this species are in Bruxelles (IRSN) and Tervuren (MRAC).

***Bequaertina marteli* (Dautzenberg, 1901)**

Figs. 37–40

Achatina marteli

Dautzenberg, 1901:3.

Ganomidos marteli

Dautzenberg, 1901, pl. 1, fig. 1.

Achatina marteli pallescens

Dautzenberg, 1901:3.

Ganomidos marteli pallescens

Dautzenberg, 1901, pl. 1, fig. 2.

Callistoplepa marteli

Pilsbry, 1905:129, pl. 47, fig. 21 (ex Dautzenberg); Germain, 1909:90; Pilsbry, 1919:81; Bequaert & Clench, 1934c:114.

Callistoplepa marteli var. *pallescens*

Pilsbry, 1905:129, pl. 47, fig. 22 (ex Dautzenberg); Bequaert & Clench, 1934c:114.

'*Achatina* sp. near *tavaresiana*'

Verdcourt, 1966:106, fig. 12; 1988:219.

Callistoplepa marteli

Germain, 1936:151; Oliver, 1983:9.

SHELL. Shell ovate-achatiniform, opaque, thin but not fragile. Whorls 6–6¼, rarely 6½. Spire moderately broad, conic; apex obtuse; only one out of 69 specimens examined had a mammillate apex. Upper whorls only slightly convex, descending proportionately but expanding somewhat more rapidly. Sutures fine and regular in nepionic whorls, shallow to moderately deep and irregular in the following whorls. Last whorl large and more convex, 80% of shell length; range for 4½–6½ whorls, 77–84% (n = 69). Aperture inverted

auriform to ovate-elongate; pale blue-white within; surface pattern and flames show through. Columella straight or weakly arcuate, somewhat slender, concolorous but with a thin calcareous film; usually moderately obliquely truncated. Outer lip thin, extending basally only a slight way below the truncation; its arc is characteristically greatest below midway in the mature specimens. Parietal callus thin but apparent even in the smaller specimens.

The nepionic whorls (first 2½) are unicolorous pale buff-white. This changes imperceptibly to a uniform dull ground colour that varies in specimens from a rather intense olivaceous yellow to subdued olivaceous. In most specimens, faint, very diffuse light castaneous blotches appear in the fourth whorl. At first these are vertical, evenly spaced and broader at their base; but they soon become fragmented apically, darker, and strikingly distorted into diagonal even spiral, irregular streaks, bands and flames that are approximately as wide as the ground colour space between them. In the present study of 69 specimens, 72% are flammate, 13% are vaguely flammate but only on the last whorl, and 15% are without flames, i.e. 'pallescent'. In some of the latter, e.g. the lectotype of *Achatina marteli pallescens*, lines of arrested growth are highlighted with thin bands of dark brown.

A delicate beaded or slightly semilunar sculpture starts in the second quarter of the first whorl and quickly assumes in the early second whorl the diagnostic sculpture of strikingly coarse, elevated, round or crescentic, discreet but tightly packed beads that are neatly aligned in 5–7 spiral rows. This pattern persists almost uniformly throughout the second whorl. In the mid-third whorl, the transverse rows become greatly compressed, producing growth wrinkles and converting the beads into transverse welts 2–3 times as long as wide. This doubtless marks the first postemergent growth. Adapertural to this, the growth wrinkles become prosocline, the sculpture gradually becomes less compressed, the spiral striae become more numerous and deeper, and the individual welts become larger, more variable in size, more rectangular, and often cleft. The remarkably evenly and closely spaced coarse growth wrinkles embrace and intensify the prosocline rows of welts, producing the characteristic prominent ribbed sculpture of this species. Apically, the ribs may bifurcate and form crenulations. Below the periphery, the welts rather abruptly reduce to one-quarter their calibre, or are absent, leaving prominently the growth wrinkles. An extremely fine decussate micromesh of the periostracum appears on the last whorl of some specimens. It is more noticeable on the shiny inner layer of the periostracum where the latter is exposed through wear or injury. It is apparent that the micromesh is formed at the time that the inner periostracal layer is laid down and that it is largely obscured by the preformed, smoother outer periostracal layer. It is likely that the micromesh assists structurally in bonding the two periostracal layers.

SOFT ANATOMY. No known alcohol preserved specimens.

TYPE MATERIAL. In his description of this species and its synonymous unicolorous 'variety *pallescens*', Dautzenberg (1901) announced that he was dedicating them to Colonel Martel and that specimens had been collected by R.P. Guillemé 'en nombreux exemplaires' in the region of Lake Tanganyika. He did not specifically designate types and paratypes, although he selected a fine flamed specimen and an equally fine unicolorous specimen that were photographed, both in apertural view only, as representative of the

two proposed taxa. These are in the type collection in Bruxelles (IRSN) and are here selected as lectotypes of Dautzenberg's *Achatina marteli* and *A.m. pallescens*, respectively (Figs. 37–40; Table 7). As he pointed out in a footnote in the original descriptions, the pronounced flame pattern of his figure 1 unfortunately did not reproduce well. Pilsbry's copies (1905) therefore reflected this deficiency. In this species, neither the lack of colour pattern nor the greater degree of ventricosity is taxonomically valid for establishing a trinomen.

In the IRSN collection there are several mixed lots totalling 48 mostly juvenile, damaged or weathered specimens. All these specimens were very carefully examined in the present study and were found to be a mixture of the flamed and unicolorous forms of this species and, in addition, juveniles of *Bequaertina pellucida* and *Achatina craveni*. These cannot reasonably be considered to have been a part of Dautzenberg's type series. Dautzenberg, however, did distribute his specimens widely. Those bearing the type locality and R.P. Guillemé as the collector are here selected as paralectotypes. The known distribution of these flamed/unicolorous specimens are BMNH 1/0, NMW 1/1, IRSN 8/5, MCZ 2/1, MRAC 7/1, NMB 2/1, MNHN 6/1, NHMW 1/0.

Table 7 *B. marteli* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Width	% whorl	% LW/L	% W/L	
6½	68.3	34.0	42.3	20.8	55.4	81	50	Mpala (IRSN) PLec
6¼	67.2	38.6	39.1	22.2	54.4	81	57	Mpala (IRSN) Lect
6	63.7	33.2	37.7	19.6	51.5	81	52	<i>A.m.p.</i> * Mpala (IRSN) Lect
6¼	62.9	32.3	36.7	18.2	49.8	79	51	<i>A.m.</i> * Mpala (MCZ) 97929 PLec
6	60.8	34.8	38.0	19.4	51.3	84	57	Mpala (MNHN) PLec
5¾	58.4	32.3	37.3	18.5	49.0	84	55	Mpala (MRAC) 5129 PLec
654.032.233.817.043.78160	54.0	32.2	33.8	17.0	43.7	81	60	Mpala (MNHN) PLec
5¾	48.4	26.9	32.1	15.0	39.8	82	55	Mpala (BMNH) PLec 1937.12. 30.1934
5½	48.4	27.9	32.0	16.7	40.5	84	58	Mpala (MRAC) 5125 PLec
6	48.4	27.3	31.0	15.5	39.6	82	56	Mpala (MRAC) 5131 PLec

Total specimens examined: 69. Sources: BMNH, IRSN, MCZ, MNHN, MRAC, NHMW, NMB, NMW.

TYPE LOCALITY. Mpala (= Pala) 6° 45' S, 29° 31' E, region of Lake Tanganyika, Zaire (cf van Burggen, 1988:9).

DISTRIBUTION. All specimens examined are from the type locality. Verdcourt kindly sent the author a photograph of a specimen, which earlier had been identified as *Achatina tavaresiana* (Pain & Verdcourt, 1962; Verdcourt, 1966). This specimen is clearly *B. marteli* and establishes this species in Tanzania on the eastern shore of Lake Tanganyika in the Mahari Peninsula at Nkungwe (= Kungwe) 6° 07' S, 29° 48' E. It was collected in 'litter in thick scrub at head of stream, altitude 4500 ft'. With the many locality records known for *B. pellucida*, including Mpala, it is strange that the distribution of the present species is, to date, so contrastingly limited.

REMARKS. This is the least fragile and the most boldly sculptured species in the genus. Phylogenetically, it appears to stand between *B. pellucida* and *B. pintoi*. Mixed lots of *B. marteli*, *B. pellucida*, and *Achatina craveni* suggest that these species are sympatric. The juveniles in particular are confusable. By far the largest series of this species is to be found in Bruxelles (IRSN).

***Bequaertina pintoi* (Bourguignat, 1889)**
Figs. 41–51

Serpaea pintoi

Bourguignat, 1889:86, pl. 4, fig. 4.

Achatina fragilis

Smith, 1899:591, pl. 35, figs. 3, 4 (*non Achatina fragilis* Deshayes, 1864); Ancey, 1902:278, text fig. 6; Pilsbry, 1904:63, pl. 9, figs. 25, 26 (ex Smith); Dautzenberg & Germain, 1914:26.

'*Achatina* . . . sp. nov?'

Ancey, 1902:277, text fig. 4.

Achatina pintoi

Pilsbry, 1904:63, pl. 41, fig. 8 (ex Bourguignat); Bequaert, 1950:11; Verdcourt, 1966:111, 1983:219.

Achatina nyikaensis

Pilsbry, 1909:113, 1919:79; Connolly, 1925:168, 1939:321; Germain, 1935:9; van Bruggen, 1965:81, 1988:10; van Bruggen & Meredith, 1984:161.

Callistoplepa nyikaensis

Bequaert & Clench, 1934c:115, 116.

Callistoplepa thielei

Bequaert & Clench, 1934c:115, pl. 2, figs. 8–10, 12.

Callistoplepa nyikaensis

Verdcourt, 1966:111, 1983:219; Meredith, 1983a:29, fig. 10, 1983b:247.

SHELL. Shell thin, fragile, highly variable in shape, usually elongate-ovate or ovate-subsuccineiform, but may be ovate, globose-ovate or slender conic-ovate. Whorls 6–6½, rarely slightly larger. Apex obtuse; vaguely mammillate in some specimens. Spire usually inscribes a short broad based triangle that appears to be nearly equilateral, 27–36% of shell length. Less commonly, the spire is more produced, with the sides of the connate triangle appearing longer than the width of the base, 37–43% of shell length; such specimens may or may not have a more slender last whorl. Sutures fine, distinct, deeply impressed, quite regular, but may be faintly crenulate in the last part of the sixth whorl. Whorls slightly, moderately, or distinctly convex, usually expanding rapidly to form a large last whorl, 84% of shell length; range for 3½–6¾ whorls, 78–87% (n = 87). Aperture ovate-acuminate; charac-

teristically widest slightly below middle; translucent pale milky opalescent within; fine, closely aligned internal riblets mirror the external sculpture. Columella concolorous or white; long, slender, feebly arcuate or nearly straight; truncated obliquely or abruptly. Outer lip extremely thin, fragile, somewhat receding, arcuately skewed and evenly rounded toward the base. Parietal callus not apparent in young or fresh specimens; thinly calcareous white in others.

Nearly 90% of the specimens examined in the present study (77/87) were essentially unicolorous in a colour gradient from pale olivaceous yellow to olivaceous brown to deep olivaceous green. In individual specimens, the colour tends to be quite uniform, except for darker bands where there was cessation of growth. Because of their very thin two periostracal layers, the apical whorls, which are pale straw colour, soon become calcareous white with wear and exposure. Ten of the specimens examined had on their lower whorls, very faint, narrow light castaneous irregular, sometimes interrupted, transverse stripes that were one-half to one-third the width of the ground colour between them. In some specimens, only a fraction of a whorl was involved.

Extremely fine spiral engraved lines appear at the end of the first whorl. Transverse lines appear in the second whorl, giving rise to depressed beads that become more conspicuous and more abundant until near the middle of the third whorl. At that point, which marks the end of the nepionic whorls, the beads become compressed into very narrow transverse ridges. In the fourth whorl, this compression is relieved and a fairly even granulose-cancellate sculpture emerges. In the fifth and sixth whorls, the granulae swell to become welts that occasionally anastomose along the transverse growth wrinkles, with the shallow spiral lines remaining strongly in evidence (cf Bequaert & Clench 1934c, fig. 12). Usually, this sculpture diminishes rapidly in caliber at the periphery, with essentially only the growth wrinkles continuing into the otherwise smooth surface. In other specimens, the sculpture may continue strongly below the periphery, but at a reduced calibre. In still others, subdued patches of this sculpture appear irregularly below the periphery, and perhaps contrastingly so with resumed growth after diapause. Particularly in the parietal area, the dull, tenaceous microscopically granular outer periostracal layer may wear off, exposing the smooth, shiny inner periostracal layer. Only rarely has a periostracal decussate micromesh been observed in this species, and then only spottedly below the periphery in the inner periostracal layer of the sixth whorl, e.g. in the holotype of *Callistoplepa thielei* Bequaert & Clench, 1934c.

SOFT ANATOMY. Alcohol preserved specimens available 29/dissected 17. Tanzania: BMNH 1/1, NHMW (no.47996) 1/1. Malawi: CMNH 13/2, HM 5/5 (all now at RMNH), NG 4/3 (2 now at BMNH), RMNH 3/3. Zimbabwe: NM 2/2. Additional Malawi specimens are in collections HM and NG. No others are known. Most specimens examined were well extended from their shells.

In the individual specimen, the body colour varies from unicolorous pale buff to dark grey. A black thin-lined, coarsely reticulate pattern is characteristically present laterally on the foot. Sole of foot is uniformly pale dusky, without variation in texture. Usually a delineated or diffuse narrow dark grey or black stripe, originating behind each ommatophore, passes posteriorly toward the mantle on either side of the paler neck region. The mantle varies from unicolorous dark or light grey to a grossly maculate pattern. The Chirinda

Forest, Mount Selinda, Zimbabwe field notes of A.C. van Bruggen *in litt.*) record the body colour varying from black to pale grey marbled with black, and the longitudinal stripes varying from white to greyish white.

The short, slender penis (P) and the slightly shorter penis sheath (PS) seem diminutive compared to the relatively gross structures of the basal female conduit. Of the 17 specimens dissected, 11 had the apical-most P and the basal-most basal vas deferens (BVD) projecting slightly above the rim of the PS. In the other 6 specimens, the P was completely covered by the PS, 2 of which were gravid, 2 were over-drowned with consequent eversion of the genital atrium (GA), one was immature and one was severely distorted because of improper fixation. There was no positive correlation in this latter group of 6 with such other possible influencing factors as latitude, shell size, length of penial retractor, month of collection or size of albumen gland. The specimen (NM) depicted in Fig. 17 collected by A.C. & W.H. van Bruggen in Zimbabwe (Vumba Circular Drive, Zonwi River Bridge) has thus been selected as representative of the first group and typical of this species.

In all specimens, the penial retractor (PR) inserts either on the anterior diaphragm, on the body wall of the neck, or at the forward junction of the diaphragm, mantle and body wall. In well extended specimens, it can appear inordinately long. Cutting and spreading the thin-walled PS reveals the slender P and BVD within (Fig. 18). Fine muscle strands pass basally from the PR to cover thinly the apical P. About half way down the P, these strands attach to the smooth, shiny inner surface of the PS and then proliferate into voluminous strands that completely cover the BVD and infuse with the tissues of the basal P and PS. At this level the tissue layers are not distinct, but below the PS the male conduit continues as a short penial atrium (PA) that joins the vaginal atrium (VA). These fuse to form the genital atrium (GA). Strap-like overlapping, glistening eversion muscle bands (EM) connect the basal male and female conduits to the inner right body wall. During precopulatory behaviour, contraction of these muscles cause the GA, then the PA and VA to evert, to protrude as a stimulatory organ, and subsequently to initiate the extroversion of the intromittent organ. In some older specimens, these bands can be so voluminous and so high on the PS that they seriously obscure relationships. The thin-walled BVD passes through the PS to emerge as a much larger, thick-walled apical vas deferens (AVD), which basally functions as an ejaculatory duct and as a support for the thin-walled everted P. About midway apically, the AVD gradually becomes thin-walled until at the AVD/FO junction, it forms a glandular funnel-shaped chamber that internally is crowded with extremely thin epithelial partitions. This may function as a secondary seminal vesicle (SSV). There is no pilaster or verge in this species.

In the basal female conduit, the vagina (V), free oviduct (FO) and the spermathecal duct (SD) form, without distinct delineations, an impressive muscular Y-shaped structure (Fig. 18). Upon dissection, the broad lumen and the prominent longitudinal plicae of the V are seen to be uninterruptedly confluent with those of the SD. In contrast, the lumen of the basal, muscular thick-walled FO is slender and it is confluent with that of the V through a small recessed pore. This arrangement ensures the passage of the intromittent organ into the SD during copulation. The thick-walled FO functions basally as an ovijector; apically its thin walls accommodate the descending eggs. The clavate-elongate

spermatheca (S) (Fig. 17) frequently is apically attenuated because thin fibers firmly attach it 4–5 mm below the AVD/FO junction. That junction, in turn, is held tightly together on the right internal body wall by fibres from the transverse myoseptum. Any contraction or extension thus provides maximum pull in this part of the body. As a result, under certain conditions, the S apex and SD may become inordinately elongate or nearly disappear into a huge sacculate S. Severe contraction of the viscera may even produce the artifact of a tandem bilobed S. The only important character of the S is its consistent position below the AVD/FO junction. The FO, though shorter than the AVD, is conspicuously long, nearly uniformly wide, and approximately twice as wide as the AVD. Although there are thin facia binding together V, SD, S, FO and AVD, there is no formation of a vaginal rententor per se.

Two specimens were gravid. One from Chinyama, Malawi (HM) was collected in February 1983 (mid-rainy season) and had 56 light yellow, moderately large eggs averaging 6.3×5.2 mm. The other, from Lake Rukwa, Tanzania (BMNH), was collected in 1938 (month not indicated) and had 51 similar eggs measuring 7×5.5 – 6.5 mm. The eggs, without discernible embryos, were closely embraced by uterine tissue folds as depicted by Mead (1950, fig. 48) for *Achatina fulica* Bowdich, 1822.

All specimens dissected showed a remarkably gross development of a trimerous hermaphroditic duct system (Fig. 19). Basally, there is a 10 mm characteristically deeply convoluted portion just distal to the talon. Next, there is a 3×2 mm discreet, compacted saccular portion that appears to be glandular. And finally, there is a 6 mm slender, weakly convoluted portion that quickly forms a series of five larger, tightly convoluted ductules leading to the five gonadal acini buried in the right lobe of the digestive gland. The talon is elongate, capitate and diminutive (1.5×0.5 mm). The spermooviduct is characteristic of the family.

The following anatomical characters distinguish this species from *B. graueri*: basal genital fascia diaphanous; AVD about twice the width of BVD and half the width of FO; P slender, much longer than wide, normally projecting slightly above PS; BVD slender, much longer than wide.

TYPE MATERIAL. For over a century, Bourguignat's (1889) *Serpaea pinto* has been an enigma to conchologists. The principal contributing factor has been the artist's rendering an excessively bold, wide, broadly truncated columella. A second factor is that the exceedingly thin, fragile shell of the only known specimen unfortunately had become broken sometime since it was drawn. The several pieces, including a figure '4' label, had been placed in a separate vial. This specimen (Figs. 41, 42; Table 8) is in Paris (MNHN) and is here considered to be the holotype by monotypy (Code Art. 73(a)(ii); 74(b). Its conchological features and the type locality in eastern Tanzania support the conviction that this is conspecific with Smith's junior subjective synonym *Achatina fragilis* (1899). Pilsbry (1904:1, 21, 63) placed *Serpaea* in the synonymy of *Achatina*, indicated (1909:113) that Smith's name was a primary homonym of Deshayes' fossil species (1864), proposed the replacement name *Achatina nyikaensis*, reproduced Smith's figures [fig. 26 is way too intensely coloured], and perspicaciously placed Bourguignat's species and Smith's species seriatim under *Achatina* in his Manual.

Smith's syntype lot of seven specimens from Nyika Plateau, Malawi, unfortunately contains a single specimen of *Achatina*

Table 8 *B. pinto* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl LW/L	% W/L	
6½	74.6	42.8	47.6	26.1	62.5	84	57 Nyika Plateau (BMNH) Lect <i>A. fragilis</i> *
6¼	74.4	42.0	46.3	24.6	61.4	82	56 Maceque (SAM)
6	66.8	40.6	46.9	24.0	58.0	87	61 Nyambadwe (NG)*
6¼	62.2	32.7	38.3	19.5	50.6	81	52 Utengule (ZMB) Holo <i>C. thielei</i> *
6	56.2	37.8	38.0	21.3	47.9	85	67 Bulawayo (RMS)
6	56.0	33.0	35.5	19.6	46.5	83	59 Utengule (BMNH)* Mac Andrew (1563)
6	53.3	27.2	33.0	16.7	43.5	82	51 Chirinda (BMNH)* 1907.7. 25.3
6	50.1	32.6	33.0	19.8	42.4	85	65 Mamboya (BMNH)* 1885.5. 25.47
6	49.7	33.6	31.8	19.5	43.2	87	68 Ngengre (MNHN) Holo <i>S. pinto</i> *
6¼	49.3	27.2	28.3	15.0	38.5	78	55 Tanzania (NHMW)*
5¾	49.3	33.7	34.9	19.3	42.7	87	68 Pemba (SAM)
5¾	43.7	29.0	29.0	17.8	37.2	85	66 Usagara (BMNH)

Total specimens examined: 92. Sources: BMNH, FMNH, HM, IRSN, LNK, MCZ, MNHN, MRAC, NG, NHMW, NM, NMW, RMNH, SAM, SMF, UMMZ, ZMB.

craveni Smith, 1881. Since Smith, as its author, was thoroughly familiar with this latter species, since he did not designate the number of syntypes, and since he separately discussed (p. 35) and figured (figs. 1–4) specimens of both this species (BMNH no.97.12.31.1–7) and *A. fragilis* (BMNH no.97.12.31.8–14) in his 1899 paper, it is here safely assumed that the division between the two adjacent accessioned specimen lots was an inadvertent curatorial error, with no nomenclatural implications for the misplaced specimen. The unicolorous, largest and finest specimen (BMNH no.97.12.31.9) of the six syntypes (Smith's fig. 3, Pilsbry's fig. 25), here shown in Figs. 43, 44 bears a handwritten note, 'Lectotype "3" A.C. van Bruggen, May 1974'. This selection is here endorsed. Other known and examined paralectotypes are single specimens in Berlin (ZMB no.101934) and Vienna (NHMW/R).

Ancey (1902) described and illustrated a specimen which he labelled '*Achatina* . . . *sp. nov.*' from Ugogo (5° 4' S, 34° 4' E). Ancey's collection was distributed widely by Geret and this specimen so far has not been located. However, the very

large aperture, the slender arcuate columella, the transverse stripes, the translucence of the shell showing the pattern through the aperture, and the locality indicate that his specimen is Bourguignat's species.

Bequaert & Clench (1934c) found nine purchased (Hermann Rolle) specimens from Utengule, Tanzania in the Berlin Museum (ZMB) that were marked as new and given a preempted manuscript name, but were undescribed. Although they felt the new taxon 'might perhaps prove to be a local race' of *Callistoplepa nyikaensis*, its more slender, more tapered shape convinced them it should be established as the new species *Callistoplepa thielei*. The largest specimen previously had been broken, so they selected the second largest specimen as the holotype (Figs. 45, 46). In addition to the holotype, they figured two paratypes. This series of four types (ZMB no. 53177) are in Berlin (Kilius, 1992). Examination of these types in Berlin in 1989, showed evidence that the paratypes had been broken apparently on their return to Berlin because their fragile shells had been stuffed excessively with cotton, leaving only the holotype undamaged. The five other original specimens, 3 full grown and 2 juveniles, are labeled paratypes (MCZ no. 98686) in the Harvard collection. Three other broken specimens with the same data are in Frankfurt (SMF); there is no evidence that these were seen by Bequaert & Clench.

TYPE LOCALITY. Bourguignat (1889) states, '... provient des environs de l'Ougeregere, vallée du Kyngani, dans l'Oukani'. Inside the lip of the holotype, in Bourguignat's handwriting, is '*Serpaea pinto* Ougeregere (Oukami). A small label bears the inscription 'M. Requin 1846 30'. According to B. Verdcourt (*in litt.*), Ukami is a large geographic district that surrounds and includes the Uluguru Mountains in Tanzania. The Kingoni river and the Ngerengere settlement and stream, however, place the type locality close to 7° 03' S, 38° 31' E, 125 km west of Dar-es-Salaam (cf Verdcourt, 1966:111).

DISTRIBUTION. This is by far the most widespread species in the genus. The 32 recorded localities define a 1800 × 1200 km territory 4–20° S, 27–39° E that includes eastern Zaire, eastern and western central Tanzania, nearly all of Malawi, south central Zambia, southern and eastern Zimbabwe, and far west central Mozambique (Fig. 16). The northern outpost of this species was established in Zaire by R. Grauer in 1910, when he found and preserved in alcohol a specimen in 'the primary forest behind bordering hills of the northwest shores of Lake Tanganyika, 1800–2200 m' (*trans.*) 4° 30' S, 29° 00' E. It is noteworthy that along the west, there is an almost straight N–S line of demarcation 27–28° E from eastern central Zaire to south central Zambia and southwestern Zimbabwe. Connolly, in his writings (1925, 1939) and on some of his specimen labels, juxtaposes the geographic names Macequece (a district in eastern central Mozambique) and Lourenço Marques (the major port now known as Maputo in southern Mozambique). Specimens may have been shipped from this port, but there is no convincing evidence that this species has ever been collected in Mozambique south of the Macequece district. The remarks of Germain (1935:4) seem to clarify when he explains that Portuguese East Africa is generally divided into two large regions separated by the Zambeze River, 'le Mozambique au Nord, le Lourenço Marques au Sud'. When adequate population studies can be

made in this widespread species, valid subspecies may emerge.

REMARKS. This apomorphic species is most closely related to *B. marteli*. Both *Achatina craveni* E.A. Smith, 1881 and *B. pinto* are highly variable and are often confused in collections, particularly where the field data are the same or the individuals are small. Despite rather considerable overlap in the extremes of the conchological characters of these two species, the shell of *A. craveni* can be differentiated on the basis of the following: nepionic whorls smooth; last whorl equals only 70–75% of shell length (vs 80–90%); one to two more whorls for the same length; apex more acute; columella much shorter, broader, straighter and more squarely truncated; finer and deeper granulate-cancellate sculpture; shell usually much less fragile.

The wide distribution and the independently great variability in shell characters, even within a single population, are responsible for the long and confused synonymy of this species. The soft anatomies of antipodal specimens, and many between, support the conclusion that only one species is involved.

Ecological notations with specimen data (HM, NG) indicate that active specimens were found in Malawi lowland evergreen forests, along the banks of earth roads, crawling on leaf litter, and on the underside of banana leaves in the rain. Specimens from Mbeya, Tanzania were found in luxuriant herbaceous vegetation (LNK). The director of the Imperial Institute of Entomology earlier reported that in the Nkoto-Kota district of Malawi there was a 'very serious outbreak in November 1937', implying that this species has the potential under certain conditions of becoming an agricultural pest. In Zambia this snail is known as 'chuzuya'.

The fine series of specimens in BMNH convincingly demonstrates the wide range of variability in the shells of this species (Figs. 41–51).

Bequaertina fraterculus (Dupuis & Putzeys, 1900) Figs. 52, 53

Ganomidos fraterculus

Dupuis & Putzeys, 1900:xiii, text fig. 18.

Callistoplepa fraterculus

Pilsbry, 1905:129, pl. 47, fig. 23 (ex Dupuis & Putzeys); Germain, 1909:90; Pilsbry, 1919:80; Bequaert & Clench, 1934c:114.

SHELL. Shell ovate-turrite, extremely thin, translucent. Whorls 6–6¼. The second and third whorls are comparatively large, long and nearly straight-sided, producing characteristically a collared blunt mammillate apex. The fourth and subsequent whorls are convex and expanded proportionately. Sutures moderately deep. Last whorl large, but not inordinately so, 78% of shell length; range for 6–6¼ whorls, 77–80% (n = 10). Aperture oval, pale milky within. Columella brown, long, slender, nearly straight, obliquely truncated. Outer lip thin, evenly arcuate; receding at base in profile. Parietal callus diaphanous.

Highly irregular castaneous streak and spot brush marks, some of which are closely highlighted with buff adaperturally, are characteristically found on the last whorl; however, these may be reduced to a few obscure dull buff spots more or less limited to the peripheral carina. The earliest signs of this diagnostic colour pattern are seen in the third whorl. The ground colour intergrades from pale horn colour of the

unicolourous nepionic whorls to an obscuring dark olive brown of the last whorl.

Faint, closely oppressed minute crescentic granulations may appear in the second half of the otherwise smooth first whorl. These granulations dominate the second whorl, giving it an evenly, delicately engraved appearance. In contrast, rather bold, diagonally oriented arcuate plicae, arising from the suture below, disrupt this sculpture in a narrow basal zone. This plication, which may start even in the last part of the first whorl, rather abruptly disappears in the third whorl, leaving a delicate, closely aligned series of nearly transverse lirae, uninterrupted except for small, sparse, ghost-like patches of granulations in some specimens. This marks the end of the nepionic whorls. In the fourth and fifth whorls, the lirae become increasingly strongly prosocline, more regular, apically arcuate immediately below the suture, and eventually so prominent that they obscure the growth lines. In the sixth whorl, the lirae become finer, less regular, more nearly orthocline, and often interspersed with short parallel lirellae. In the fifth whorl, spiral lirae, which seem to join rather than interrupt the prosocline lirae, appear somewhat irregularly, producing a slight checkerboard effect, reminiscent of the sculpture of *Achatina tracheia* Connolly, 1929. These spiral lirae, which are quite close together near the suture, irregularly diminish in number and intensity toward the columella. Very shallow malleations, starting subtly in the fourth whorl, intensify the checkerboard effect. A subdued but apparent carina appears at the periphery, where the lirae are seen to bend slightly. The carina is more conspicuous in the younger specimens. Abrasion of the shell along the periphery and along some of the more prominent lirae visually intensifies the carina and the sculpture by exposing the brilliantly shiny inner periostracal layer. The outer layer of the periostracum imparts a characteristically dull, corneous luster to the shell.

SOFT ANATOMY. No known alcohol preserved specimens.

TYPE MATERIAL. Nine of the ten known specimens of this rare species were collected by Dupuis and are considered syntypes. Six of these were identified and labelled as 'cotypes': three in Tervuren (MRAC no.5140–5142) and three unnumbered specimens in Bruxelles (IRSN, General Collection). The seventh specimen (MRAC no.5139) was labelled as the one figured by Dupuis & Putzeys (1900); their figure 18 (reproduced by Pilsbry, 1905) is so generalized that it cannot specifically identify with any of the syntypes. Unfortunately, the apex of this specimen had been broken and cemented together, with a resultant alteration of the shell configuration and length. The damage possibly occurred during the precarious period when the artist had the specimen. Two additional syntype specimens (IRSN) were given to Dauzenberg by Dupuis, one of which was collected in Nsendwe. Under these circumstances, and since the authors did not designate a holotype, the largest and finest of the four MRAC syntypes (no.5140) is here selected as the lectotype of Dupuis & Putzeys' *Ganomidos fraterculus* (Figs. 52, 53; Table 9). The tenth known specimen, acquired by Preston, was passed on to V.W. MacAndrew, and is now in the BMNH. Its apex was damaged and repaired naturally. This, too, most probably was collected by Dupuis and should be considered a paralectotype.

TYPE LOCALITY. The Island of Mvula on the Lualaba River, Zaire. J.C. Bequaert was unable to find this locality on any map (Pilsbry, 1919:11, 19), nor is it listed in the

Table 9 *B. fraterculus* – Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Aperture Width	Last whorl	% LW/L	% W/L	
6	51.0	28.7	30.0	16.4	40.7	80	56	Mvula (BMNH) PLec
6	50.5	29.0	30.0	16.9	39.3	78	57	Mvula (IRSN) PLec
6¼	50.4	28.5	30.5	17.0	38.9	77	56	Mvula (MRAC) 5140 Lect*
6	47.5	27.4	27.8	16.0	37.5	79	58	Mvula (MRAC) 5139
6	46.3	26.8	28.7	15.5	36.7	79	58	Mvula (MRAC) 5141 PLec
6	44.4	26.6	27.2	14.8	35.0	79	60	Nsendwe (IRSN) PLec
6	44.3	26.4	26.7	14.5	34.0	77	59	Mvula (IRSN) PLec
5¾	40.2	26.4	26.2	14.2	32.6	81	66	Mvula (MRAC) 5142 PLec
5¾	37.5	23.0	22.6	13.2	29.7	79	61	Mvula (IRSN) PLec
5¾	36.5	21.7	22.0	12.2	28.2	77	59	Mvula (IRSN) PLec

Total specimens examined: 10. Sources: BMNH, IRSN, MRAC.

current USBGN series. The only lead is the fact that a single specimen of this species in the Dautzenberg collection (IRSN) bears the data: 'Nsendwe, Congo. P. Dupuis Coll., leg & ded'. At the same time that Dupuis & Putzeys described *Ganomidos fraterculus* (1900), they described the new species *Perideriopsis mvulaensis*, giving its locality as 'île de Mvula (en face de Nsendwe)'. Bequaert in Pilsbry lists Nsendwe as 3° 05' S, 26° E. This location nearly coincides with the important crossroad Kindu-Port-Empain 2° 57' S, 25° 56' E, hence Mvula must be very close to 3° S, 26° E.

DISTRIBUTION. The two known localities for this species are the Island of Mvula and the nearby onshore village of Nsendwe in Zaire. Given the nature of the riverine environment, this species may well be found on other of the many small islands and possibly in shore sites along this northward flowing remote section of the Lualaba.

REMARKS. Phylogenetically, this species appears to stand between *B. graueri* and the plesiomorphic *B. pellucida*. Based on a single specimen from Nsendwe (BMNH, Preston 'L/K 13/11/01'), *B. pellucida* may be sympatric with *B. fraterculus*.

Bequaertina graueri (Thiele, 1911)
Figs. 54–57

Achatina graueri

Thiele, 1911:205, pl. 5, fig. 43; Pilsbry, 1919:78.

Achatina (Cochlitoma) graueri

Pilsbry & Cockerell, 1933:366, pl. 1, fig., 1, 1a.

Callistoplepa graueri

Bequaert & Clench, 1934c:115.

Callistoplepa graueri

Schouteden, 1935a:110; 1935b:287; Oliver, 1983:9.

Callistoplepa babaulti

Germain, 1936:151, text fig. 46.

SHELL. Shell lacrimoid-subsuccineiform; the thick, durable periostracum appears to provide more support than the thin calcareous shell. Whorls 6–6½, rarely 7. Spire tapered, mammillate, elevated-conic, clearly shorter than aperture length. The first 1½ whorls form a bluntly obtuse dome. The second and third whorls expand only slightly, but descend rapidly; this produces the strongly mammillate apex. The fourth and following whorls descend proportionately, are increasingly more convex, but expand rapidly to produce an inordinately large last whorl. Sutures moderately deep, increasingly so between fifth and sixth whorls. Last whorl 80% of shell length; range for 5–7 whorls, 77–83% (n = 50). Aperture oval to elongate; very thin blue-white shelly layer within. Columella markedly slender, almost entirely concolorous, slightly arcuate or nearly straight; typically very narrowly and obliquely truncate. Outer lip thin, usually somewhat obscured by the more rapidly advancing thick periostracum, which tends to curl into the aperture in dried specimens. The arc of the outer lip is often greatest below midway and basally extended well below the columellar truncation in the more mature specimens. Parietal callus appears to be virtually absent in the smaller specimens and barely visible in the larger and older specimens.

The first three whorls are unicolorous beige-buff to buff-horn colour. Faint, diffuse wide transverse castaneous bands may emerge in the second whorl and become darker, more conspicuous and fragmented in the third and fourth whorls. These gradually give way to narrow transverse bands of various shades of brown, irregularly appearing coincident or alternating with growth bands. The darkest, broadest bands usually indicate interrupted growth. In some specimens the transverse bands may be essentially absent. Ground colour varies within and between specimens in a spectrum of olive-buff, light yellow-brown, olivaceous brown and medium dark brown. The fifth whorl often has a contrastingly paler ground colour; hence, a 5-whorl specimen, with its short last whorl, may appear to be a different species.

Pronounced spiral striae, usually 5–7, starting in mid-first whorl are offset by beaded or semilunar granules that are irregular in size and not aligned in vertical rows. The spiral rows of granules increase to 12–17 or more and the now very small granules become more uniform, more prominent, and gradually more transversely aligned in the second and third whorls. At the end of the third whorl, there is a prominent delineation that marks the end of the nepionic whorls. At this point, the granulate sculpture is rather abruptly taken over by thin, slightly prosocline growth wrinkles that increase in size and number until they dominate in the fourth whorl. In the fifth whorl, there is a reemergence of the granulate sculpture in the form of notched, subquadrate, tile-like plates that often resemble the block letters K, H, W, V, Y & M, as is strikingly seen in *Achatina reticulata* Pfeiffer, 1845. This reappearance of the granulate sculpture, accentuated by the deeper spiral striae, dominates the fifth whorl, although the growth wrinkles continue to increase in calibre and become

subcrenulate apically. In the usually somewhat darker coloured last whorl, the granulate sculpture is once again greatly reduced, but may be highlighted here and there by an isolated sporadic deep section of a spiral stria. The earliest malleations appear subtly in the third or fourth whorl and intensify in the following whorls. They consist of usually short spiral or diagonal ridges that join or distort the growth wrinkles to form a coarse, irregular raised network of welts. Often entering into this is a very faint elevation at the periphery, below which the otherwise nearly uniform sculpture is reduced. An occasional specimen is entirely without malleations. Their irregular appearance is probably explained by thin shell, tough periostracum, and environmental impacts. Continued shell deposition from within 'fixes' the dents in place. Rarely is the outer layer of the thick periostracum broken enough to reveal the shiny inner layer.

SOFT ANATOMY. Alcohol preserved specimens available 82/dissected 9. Zaire: MRAC (Mulungu, no.204.632–633) 2/2; (Kahusi-Tshibati no.610.302–305, 342–343) 79/6; ZMB (lectotype) 1/1. Unfortunately, all dissected specimens except the lectotype, were exposed excessively to formalin during their preservation; thus, even with prolonged special treatment, their tissues remained hard and the specimens were exceedingly difficult to dissect. Pilsbry and Cockerell (1933) described the living animal as very pale ochreous with head and broad based tentacles faintly bluish.

Clearly, the most conspicuous and characteristic aspect of the basal genital conduits is the vaginal retentor (VR) muscle system, grossly dominating in ventral view (Fig. 20). Slender, parallel, glistening, partly fused muscle bands pass ventrally from the vagina (V) to the right body wall along a dorsolateral line from immediately posterior to the genital aperture to the junction of the mantle and the right body wall. From the left side of the vagina, this system gives rise to a series of muscle bands that starts at the penio vaginal angle and binds tightly together the equally prominent apical vas deferens (AVD) and the free oviduct (FO). A more bold series of distinct, but laterally fused muscle bands pass from the left lateral aspect of the AVD to the same right dorsolateral line of attachment, further obscuring the basal genital structures. (These bands are shown cut short in this figure.) Apically this whole muscle system is reduced largely to a thin, transparent membrane attached to the junction of the AVD and the FO. At this same junction, a similar membrane passes to the spermatheca (S) and attaches it to the FO. The S is proportionately extremely large in this species. In four of the nine specimens examined, the slender apex of the S is folded back on itself, as shown here; this is apparently a common artifact of preservation. In the rest, the apex is extended, and although it may appear to go apically beyond the junction of the AVD and FO, it is not attached to the spermoviduct (SO) as it is in many achatinids. The spermathecal duct (SD) is so short and broad that when the S is gorged, it seems to be sessile on the V.

Short, often diagonal or anastomosing muscle bands, separate or combined, are found at the base of the penis sheath (PS) and the V. These eversion muscle bands (EM) initiate the precopulatory extroversion of the genital atrium (GA). The PS normally completely envelops the short, diminutive penis (P); in only one of nine specimens, the apical P projected slightly. The penial retractor (PR) has its origin on the apical P and inserts on the mid-forward diaphragm at or near the junction with the body wall. A single specimen,

shown here, had a bifurcate insertion; a multiple insertion is not rare in the achatinids. At the origin of the PR, the muscle fibrils enshroud smoothly and completely the apical P and the robust basal vas deferens (BVD), greatly obscuring the relationships in the basal male conduit (Fig. 21). Contributing to this, the PS is free from the P only in the approximate upper half of the left side. On the right side, fibrils from the PR extend basally to form a dense webbing that seems to invade the substance of the outer wall of the P and the inner wall of the PS. Below the PS, this infusion of tissues, along with the EM, obscurely defines the wall of the penial atrium. This atrium connects the lumina of the P and GA (Fig. 22). The lumen of the P is thickly carpeted with vermiculate rugae, which become slender and elongate near the GA, resembling the plicae of the basal V. No verge or pilaster is present. Eccentrically in the apex of the P, a small aperture leads to the narrow lumen of the extremely thick-walled BVD and AVD. These two structures provide the physical support for the extroverted, highly expansile P. Since they have supportive and ejaculatory functions, they may explain the extreme development of the VR. Approximately 8–10 mm basal to the junction of the AVD and FO, the lumen of the AVD enlarges considerably and forms an elongate, thin-walled chamber, which conceivably functions as a secondary seminal vesicle (SSV). Apically this chamber becomes saccular with thin elongate rugae.

A single specimen (610.343) was gravid. Six large, fully formed eggs, 9.5×6.5 mm, were in the apical (oviductal), cream coloured portion of the spermiduct; no eggs were in the contrastingly light brown uterine basal portion. This specimen and the five others in the same lot had robust, mature coloured, fully formed reproductive tracts. The field data thus indicate that in the Kivu, breeding takes place in October.

Kidney is large, typical of the subfamily, broad anteriorly and truncated posteriorly. Five ovotestis acini are embedded in the columellar surface of the right (apical) lobe of the digestive gland. The inconspicuous anterior aorta is on the left posterior surface of the lung, where it penetrates the diaphragm. The hermaphroditic duct, similar to that of *B. pinto* (Fig. 19), is trimerous with an abruptly enlarged saccular central portion, 5.3×2.4 mm.

The following anatomical characters distinguish this species from *B. pinto*: basal genital fascia gross, forming a VR with a massive system of muscle bands; AVD, BVD and FO are all about the same width; P is strikingly short and stubby, normally retained entirely or nearly entirely within the PS; BVD wide, about as long as wide.

TYPE MATERIAL. Thiele (1911) described this species from a single mature specimen (ZMB no.101937) in the Schubotz collection and two small juvenile specimens from the Grauer collection. The mature specimen is nearly full grown but only moderately large (Figs. 54, 55; Table 10). Thiele's fine line illustration shows it slightly larger than natural size in apertural view only. This specimen, whose soft parts are in alcohol, I labelled as the lectotype of Thiele's *Achatina graueri* when I examined it in East Berlin (ZMB) in August 1989. At that time, the single available very dark coloured juvenile specimen (Table 10) therefore was labelled paralectotype. Since then a second small paralectotype has been found there and so labelled by Kilius (1992).

Germain (1936), without any apparent knowledge of Thiele's species, described and figured the junior subjective

synonym *Callistoplepa babaulti* from two specimens collected by Babault in Kitembo, Kivu, comparing it only with *C. marteli*. The two Paris syntypes (MNHN) are large, typical specimens of *Bequaertina graueri* (Table 10). The larger, finer specimen is here selected as the lectotype of Germain's *C. babaulti* (Figs. 56, 57).

TYPE LOCALITY. Idjwi Island (= Kwidschwi, Kwidjwi, Idjewi), Lake Kivu, Zaire $2^{\circ} 09' S$, $29^{\circ} 04' E$.

DISTRIBUTION. This species occupies a 450 km long, narrow, north-south corridor in the upper Rift Valley of Zaire between Beni and Uvira (Fig. 16). So far, it has been found only as far west as Kitembo and projects slightly east of Zaire into Lobengera Mission, Rwanda and into Ibanda, Uganda. Eventually, it will also be found in Burundi.

REMARKS. This is the largest and most distinctive species in the genus. It is most closely related to *Bequaertina fraterculus*. Because of its size and colour, and because in some localities it is sympatric with *Achatina stuhlmanni* von Martens, 1892, it has been confused with that species. However, since *A. stuhlmanni* has a shorter, broader spire, a more obtuse apex, and a distinctive spirally fine-combed wavy sculpture (Bequaert & Clench, 1934a:3), it can readily be

Table 10 *B. graueri* - Representative shells measurements.

Whorls	Length	Greatest Width	Aperture Length	Last Whorl Width	% LW/L	% W/L	
7	93.2	45.7	52.3	26.6	71.8	77	49 Katana (MRAC) 610.304
6 1/4	89.7	47.0	55.5	28.4	72.6	81	52 Tshibinda (MRAC) 5115
7	89.3	43.6	50.7	25.5	70.0	78	49 Katana (MRAC) 610.302
6 1/4	78.4	42.5	46.8	24.3	62.5	80	54 Kitembo (MNHN) Lect C. <i>babaulti</i> *
6	77.0	38.6	45.9	23.5	63.0	82	50 Uvira (MRAC) 607.170
6 1/4	71.8	41.4	41.9	23.4	56.1	78	58 Kitembo (MNHN) PLec C. <i>babaulti</i>
6	62.0	36.5	37.8	20.6	49.1	79	59 Idjwi (ZMB) 101935 Lect A. <i>graueri</i> †*
5 3/4	49.8	29.1	31.8	16.4	40.0	80	58 Idjwi (MCZ)
6	49.2	22.8	31.0	14.5	39.5	80	46 Beni (MRAC) 5119
5 1/4	42.0	25.7	27.0	14.0	33.0	78	61 Idjwi (ZMB) 101936 PLec A. <i>graueri</i>

Total specimens examined: 54. Sources: IRSN, MCZ, MNHN, MRAC, NMW, RMNH, SMNH, UMMZ, ZMB.

distinguished. Pilbry & Cockerel (1933) reported seeing two living specimens 'crawling about 5 feet up on the trunk of a tree in the forest above Tshibinda at about 2100 m' in Zaire. The largest collection of this species, including many alcohol specimens, is to be found in Tervuren (MRAC). *B. graueri* is the type species of the genus.

Radulae and jaws

D'Ailly (1896:69) was the first to describe and illustrate the radulae of *Callistoplepa shuttleworthi* and *C. barriana*. Pilbry (1904:ix, xv) referred to d'Ailly's work but reproduced only the illustration of the latter species. He also reported (p. 72) that G. Schacko (1881) (*nec* 'Schako') found 'A. *pulchella* has . . . a very small central tooth'. The present work shows Schacko's specimen was therefore misidentified. Thiele (1929:560) examined and illustrated in part the radula of *C. shuttleworthi*. He also examined but did not illustrate the radula of *Leptocala mollicella* and pointed out that the middle tooth was a little smaller than the neighbouring teeth. Possibly on the basis of this observation, he prophetically juxtaposed '*Callistoplepa*' and *Leptocala*. More recently, Ortiz & Ortiz (1959:47) also illustrate the radula of *C. shuttleworthi*, but the focal plane of the microscope was apparently too low and the configurations of the teeth are misleading. The radulae in the present project were prepared according to the recommendations of Solem (1972) and the emphasis has been placed on the rachidian teeth and the adjacent laterals.

Because the soft anatomies of the four callistoplepine species are so similar, it was not surprising to find the radulae of *C. barriana*, *C. shuttleworthi* and *L. mollicella* (Figs. 58–63) to be remarkably similar. This fact supported the earlier decision to conserve intact the odontophores of the two extant soft anatomy specimens of *L. petitia*. It is assumed with confidence that the radula of this latter species is essentially like the others. In those examined, all have bold rachidian basal plates and a broad functional rachidian tooth that is one-half to two-thirds the size of the adjacent lateral teeth. A second type of tooth is found in the first series of laterals, which similarly consists of broad, solitary mesocones, but with conspicuous laterally asymmetrical basal plates. A third type of tooth arises in the second series of laterals, wherein the mesocones angle increasingly more mesad and small ectocones gradually arise. These merge almost imperceptibly into a fourth type, the tricuspid marginals with minute irregular endocones, broad shorter serrate mesocones, and increasingly reduced basal plates that no longer contact the teeth posterior to them. The greatest irregularity within and between specimens occurs in the gradient between the bicuspid laterals and the tricuspid marginals. Hence the following formulae (tooth numbers from centre to right) are only approximate: *C. barriana* C-31–55–84, *C. shuttleworthi* C-17–28–49, and *L. mollicella* C-19–28–66.

The available radula specimens in only two of the five *Bequaertina* species have produced an incomplete and somewhat confusing picture in this genus. The basal genital systems of *B. pinto* and *B. graueri* are fundamentally similar – both reflecting affinities with the Zaire Basin subgenus *Achatina* (*sensu* Bequaert, 1950). It thus was anticipated that the radulae also would be similar. The radula of *B. pinto* (Figs. 64, 65), not surprisingly, was found to be of the same type as that of *Achatina craveni* E.A. Smith, 1881 (Figs. 68, 69). Both have greatly diminished, essentially nonfunctional

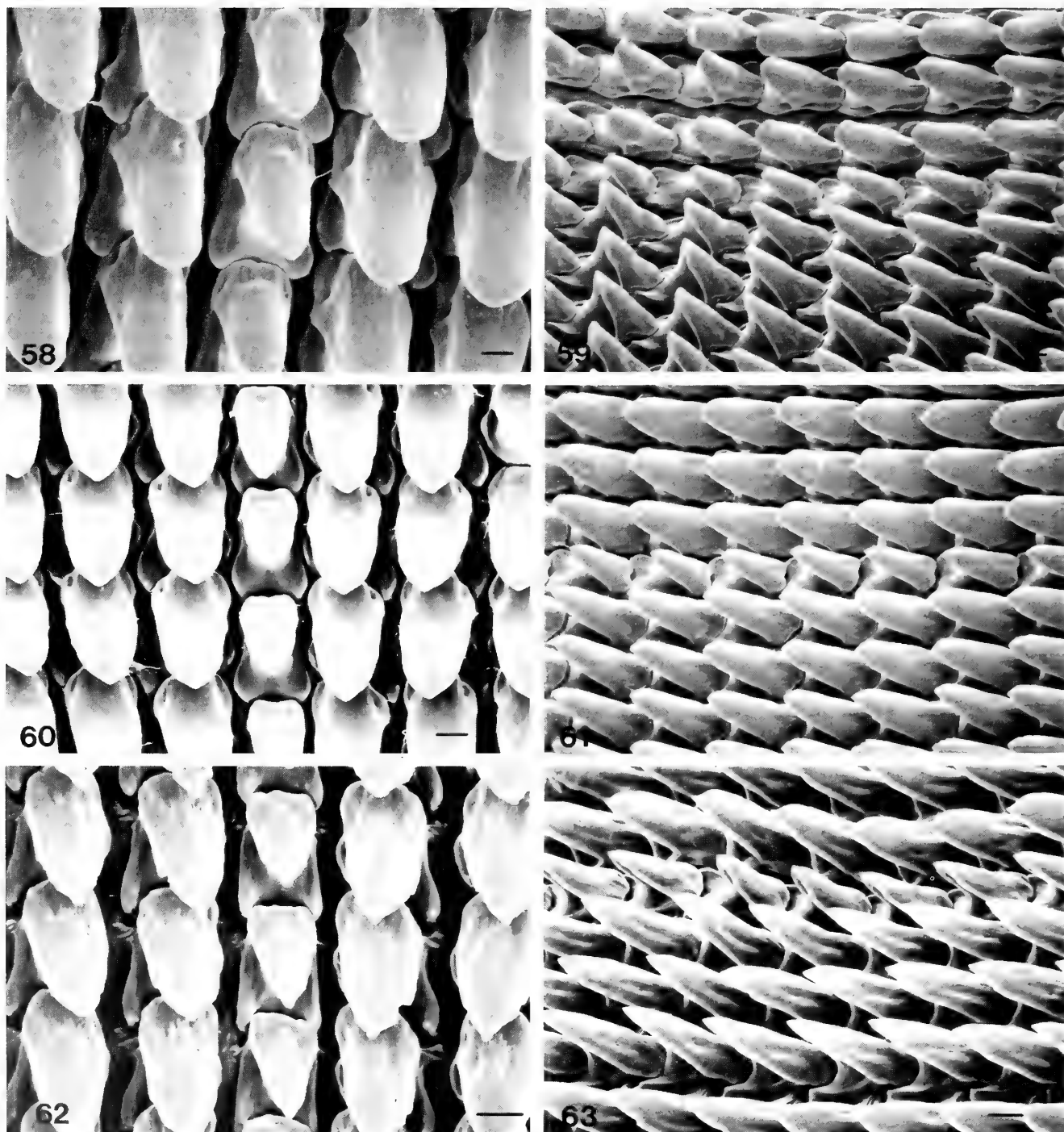
rachidian teeth that are almost concealed by the adjacent laterals. And both have broad based, nearly tricuspid laterals with angular ectocones, broad mesocones and endoconal flanges. In addition, the mesocone column of each lateral tooth directly contacts and supports the broad basal plate of the tooth immediately posterior to it. It should be noted that *A. craveni*, on the basis of its soft anatomy, belongs in Bequaert's subgenus *Achatina* rather than where he has placed it in his subgenus *Lissachatina*. The surprise came in the radula of *B. graueri* (Figs. 66, 67), with its large functional rachidian tooth, attenuated massive basal plates, more restricted contact support between horizontal rows of teeth, and an imperceptible gradient into the marginal teeth. Within the genus, *B. pinto* and *B. graueri* are at the conchological, geographic and ecological antipodes. The known plasticity in molluscan radulae suggests that undetermined different feeding demands in dissimilar habitats have produced the contrasts in the radulae of these otherwise two closely related species. *B. graueri* and *B. fraterculus* appear to be very closely related conchologically. There is a question now whether the radulae will support this assumption. In reality, the relationships in *Bequaertina* will not be understood until both the soft anatomies and radulae of *B. fraterculus*, *B. pellucida* and *B. marteli* are known. Radula formulae: *B. pinto* C-42–25, *B. graueri* C-59, *A. craveni* C-34–24.

The castaneous callistoplepine jaw forms an unusually broad middle section that quickly tapers on each side to about half its width and curves inward at the ends into a collariform structure. Its surface is featureless except for microscopic horizontal growth increments best seen under transmitted light. Measurements: *C. barriana* 2×1.3 mm, *C. shuttleworthi* 1.5×0.6 mm, *L. mollicella* 1.7×0.4 mm. The illustration of Ortiz & Ortiz (1959:46) for *C. shuttleworthi* appears excessively broad.

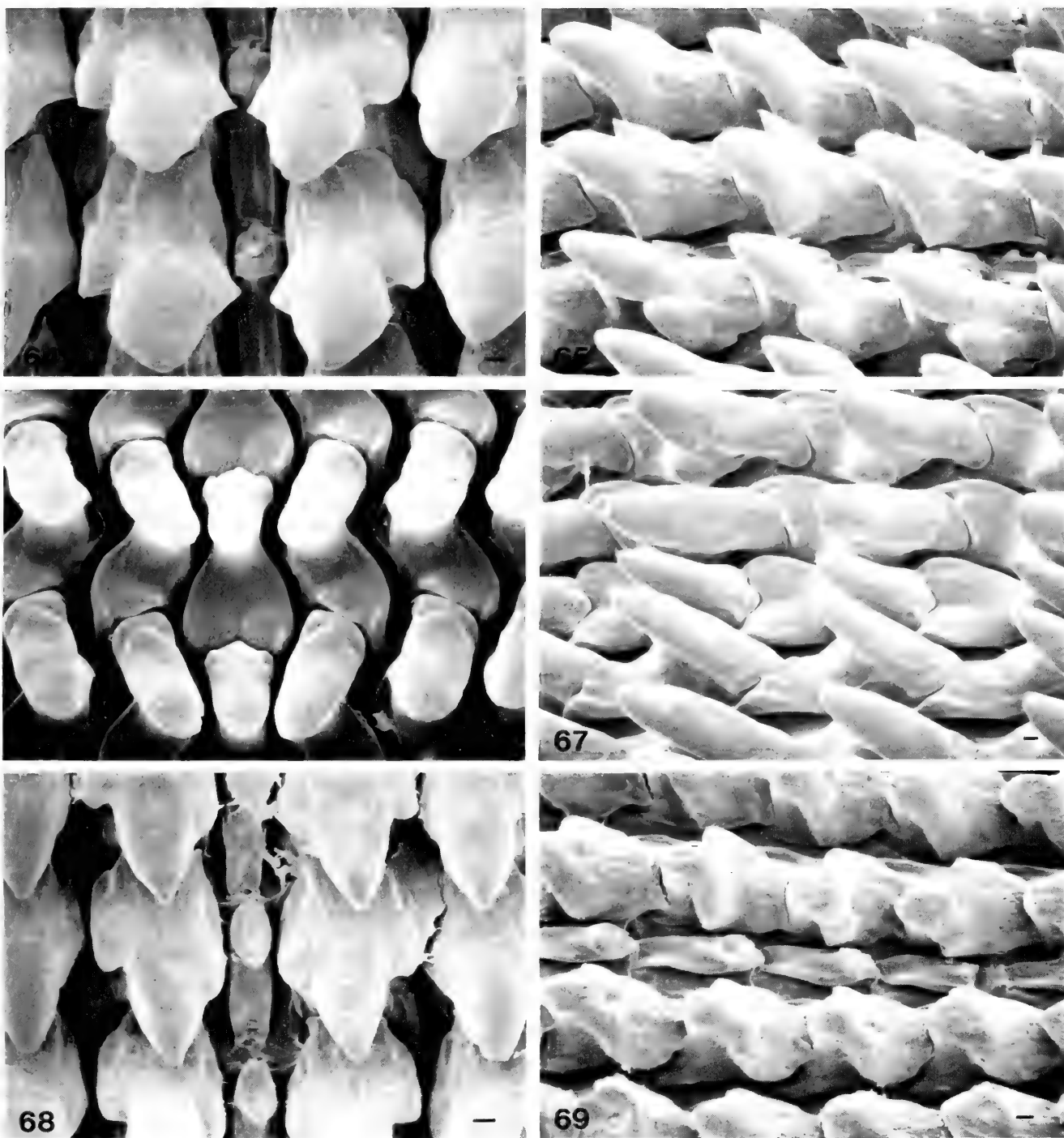
The jaw of *B. pinto* forms a light castaneous nearly uniformly slender rainbow arc, 5.5×1.1 mm, with ca 36 irregularly placed vertical ridges. In *B. graueri* the jaw forms a lower arc, 4.4×1.3 mm, with very obscure vertical lineations.

The more slender jaw of *A. craveni* forms a fulvous, somewhat depressed arc, 4.5×0.7 mm, with ca 35 fairly uniformly distributed vertical riblets.

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Figs 58–63 Dorsal and dorso-right lateral views of radulae: 58, 59 *Callistoplepa barriana* (SMF, O. Boettger). 60, 61 *C. shuttleworthi* (SMNH no. 10). 62, 63 *Leptocala mollicella* (MRAC no. 795.638).



Figs 64, 65 *Bequaertina pinto* (BMNH no. 1953.8.15.562–564, mixed lot). **66, 67** *B. graueri* (MRAC no. 204.633). **68, 69** *Achatina craveni* (BMNH no. 1953.8.15.562–564, mixed lot). Bar scale = 1 μ m.

ACRONYMS – INSTITUTIONAL & PERSONAL COLLECTIONS

AMNH	New York: American Museum of Natural History (W.K. Emerson)
ANSP	Philadelphia: Academy of Natural Science (A.E. Bogan)
BMNH	London: British Museum (Natural History) (P. Mordan, F. Naggs)
BV	Kew, Royal Botanic Gardens: Bernard Verdcourt
CMNH	Pittsburg: Carnegie Museum of Natural History (J.E. Rawlins)
FMNH	Chicago: Field Museum of Natural History (A. Solem)
GNM	Göteborg: Naturhistoriska Museet (I. Levinsson, H.W. Waldén)
HM	Newquay, Cornwall, England: Hazel Meredith
IRSN	Bruxelles: Institut Royal des Sciences Naturelles (J. van Goethem)
LNK	Karlsruhe: Landessammlungen für Naturkunde (H.W. Mittmann)
MCZ	Harvard: Museum of Comparative Zoology (K.J. Boss)
MNHN	Paris: Muséum National d'Histoire Naturelle (S. & A. Tillier)
MRAC	Tervuren: Musée Royal de l'Afrique Centrale (P.L.G. Benoit, F.A. Puylaert)
NG	Blantyre, Malawi: W. Noel Gray
NHMB	Bern: Naturhistorisches Museum (J.J. Oberling)
NHMW	Wien: Naturhistorisches Museum Wien (E. Wawra, O.E. Paget)
NM	Pietermaritzburg, South Africa: Natal Museum (R.N. Kilburn)
NMB	Basel: Naturhistorisches Museum (C. Stocker-Unterländer)
NMW	Cardiff: National Museum of Wales (A. Trew, P.G. Oliver)
RMNH	Leiden: Rijksmuseum van Natuurlijke Historie (A.C. van Bruggen, E. Gittenberger)
RMS	Edinburgh: The Royal Museum of Scotland (D. Heppell)
SAM	Cape Town: South African Museum (J. Pether)
SMF	Frankfurt: Forschungsinstitut Senckenberg Natur-Museum (R. Janssen)
SMNH	Stockholm: Naturhistoriska Riksmuseet (A. Warén, C. Holmquist)
UHZI	Hamburg: Universität Zoologisches Institut und Museum (R. von Cosel)
UMMZ	Ann Arbor: University of Michigan Museum of Natural History (J.B. Burch)
USNM	Washington, D.C.: U.S. National Museum of Natural History (R. Hershler)
UUZM	Uppsala: Universitets Zoologiska Museum (Å. Franzén, L. Wallin)
ZMB	Berlin: Museum für Naturkunde der Humboldt-Universität (R. Kilias)
ZMUC	København: Zoologisk Museum – Universitet (J. Knudsen, T. Schiøtte)
ZSM	München: Zoologische Staatssammlung (R. Fechter)

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On Recent species of *Spiraserpula* Regenhardt, 1961, a serpulid polychaete genus hitherto known only from Cretaceous and Tertiary fossils

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SYNOPSIS. A group of Recent serpulid species related to the genus *Serpula* Linnaeus, 1758, but differing from it in two important characters, is described in this paper. The first is a hitherto undescribed character, namely, the possession of internal tube structures which consist of longitudinal ridges and other structures, the form and arrangement of which, in combination with characters of the worms themselves, served to separate the various species. The second is that the thoracic membranes of the two sides in the worm do not unite ventrally at the end of the thorax to form a flap or apron as in *Serpula*. These characters are also common to 18 species, including three previously described ones. On the basis of the tube structures, these Recent species can be referred to the genus *Spiraserpula* Regenhardt, 1961, which was previously known only from fossils (Pillai, 1993). Scissiparity was observed in at least three of its species. A key to the known Recent species of *Spiraserpula* and a discussion on the systematics of the genus are included.

INTRODUCTION

In the course of a study of the serpulids currently referred to the genus *Serpula* Linnaeus, 1758, it was observed that the worms of larger species could frequently be extracted undamaged from the anterior ends of their tubes with a pair of fine forceps, while they were invariably damaged in the process in certain small species as, for instance, in the well-known Mediterranean species *Serpula massiliensis* Zibrowius, 1968. In almost every collection of the latter, the worms which had been previously extracted from their tubes were incomplete posteriorly, and the ends of their longitudinal musculature

provided evidence of their having been forcefully broken off from the rest of the abdomen. The cause of the difficulty in extracting complete worms was revealed by opening their tubes carefully from their anterior ends all the way to their posterior ends. It was found that the posterior end of the abdomen was retracted very tightly into the posterior coiled part of the tube and, quite surprisingly, against a longitudinal row of sharp serrations projecting from the inside of the tube. Examination of more material showed that these were consistent for *S. massiliensis*.

Study of similar material from various other geographical localities revealed the existence of species with other forms of internal tube structures. Evidently, these serve for anchorage

of the worm when withdrawn into the tube, and thereby, have an additional protective function. The form and arrangement of the internal tube structures, in combination with characters of the worms themselves, served to separate the various species. They are absent in *Serpula* Linnaeus, 1758, and have not been described in any of the other known genera of Serpulidae. They differ from the transverse tabulae of certain serpulids, an account of which is given by Lommerzheim (1979). Another important character common to the group is that, unlike in *Serpula*, the thoracic membranes of the two sides are not united posterior to the thorax to form a ventral flap or apron.

In the search for a name for this group, the genera *Pseudoserpula* Straughan, 1967 and *Proto-serpula* Uchida, 1978, were considered, among others. The former was found to be invalid, and an account of the study which led to this conclusion is provided under *Spiraserpula minuta*, (Straughan, 1967), in this paper. It was not possible to examine the type specimen of *Proto-serpula* to establish whether it has ITS or not. It is not in the National Science Museum, Tokyo, and other efforts to locate it were unsuccessful.

H. Zibrowius of Station Marine d'Endoume, Marseille, who went through the manuscript of this paper, and the second author discussed the group with M. Jäger of Rohrbach Zement, Dotternhausen, Germany, who re-examined the fossil serpulids studied by him (Jäger, 1983), and other material, and found that some of them too possessed internal tube structures, although they had not been reported earlier. The collaboration which followed (pers. comm.) led to a study of likely Cretaceous and Tertiary serpulid genera and species (Pillai, 1993), which revealed that the group belongs to the genus *Spiraserpula* Regenhardt, 1961, previously known only from fossil species. *Spiraserpula* Regenhardt, 1961, has priority over *Proto-serpula* Uchida, 1978, even if the latter were to possess internal tube structures, henceforth referred to in the text as ITS (*vide* Jäger 1993)). Zibrowius (1972) described a Recent spirorbid species belonging to the genus *Neomicrobis* Rovereto, 1904, which was previously known only from Cretaceous and Tertiary fossils.

In three of the Recent species of the genus *Spiraserpula* definite proof of asexual reproduction was found, in the form of branching tubes, corroborated by the presence of a parent with a schizont in one tube of *Spiraserpula snellii* sp. nov. Asexual reproduction had previously been reported for the genera *Filograna* Berkeley, 1835, *Filigranula* Langerhans, 1884, *Josephella* Caullery & Mesnil, 1896, *Salmacina* Claparède, 1870 and *Rhodopsis* Bush, 1905 (ten Hove, 1979; Ben-Eliahu & ten Hove, 1989). Pillai (1993) reports the occurrence of tube branching in the fossil species *Spiraserpula versipellis* Regenhardt, 1961. It would not be surprising if it turns out that scissiparity takes place in most, if not all, species of the genus *Spiraserpula*, in view of their aggregated occurrence.

Nineteen species of *Spiraserpula*, including the three known ones referred to above and an unnamed one, are described. They come from the Mediterranean, Madeira, Canary and Cape Verde Islands, Gulf of Mexico, the Caribbean and Panama, the northern Red Sea, Mozambique, the eastern islands of Indonesia, Eastern Australia, Japan and New Caledonia.

METHODS AND MATERIALS

The tubes and their internal structures, as well as whole worms and parts were examined and drawn under a stereo microscope fitted with a drawing attachment. Measurements were taken with a pair of fine dividers against a scale having an accuracy of 0.5 mm, of total length of the tube when possible, external diameter of the tube, total length of the worm, width of the thorax just posterior to the pair of collar fascicles, length and diameter of operculum, length of the opercular peduncle, and length of the longest radiole and its pinnule-free tip when present. Radioles and thoracic segments were counted on both sides, while the abdominal uncinal tori of one side were counted to determine the number of abdominal segments. The chaetae were mounted in polyvinyl lactophenol or aquamount and figured under the oil immersion lens of a high power microscope fitted with a drawing attachment. Measurements of chaetae were made with an eyepiece micrometer standardised with a stage micrometer. Scanning electron micrographs of chaetae of some of the species are also provided (Plates 1–5).

The sources of material have been detailed under the respective descriptions as well as the acknowledgements. Full details of E. Atlantic stations surveyed by the 'Tydeman' Canary and Cape Verde Islands Expeditions of 1980, 1982 and 1986 (CANCAP-IV, VI and VII), (e.g. CANCAP 4.D14, 6.134) can be found in van der Land (1987); of E. Indonesian stations sampled during the Indonesian-Dutch Snellius II Expedition (e.g. Snellius II 4.051) in van der Land & Sukarno (1986). The following abbreviations have been used in the text: AM: Australian Museum, Sydney; AMNH: American Museum of Natural History, New York; BM(NH): British Museum (Natural History), London, presently, The Natural History Museum, London; FSBC I: Florida Department of Natural Resources, Invertebrate collection, St. Petersburg, Florida; HUJ: The Hebrew University, Jerusalem; MCZ: Museum of Comparative Zoology, Harvard; NNM: Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Natuurlijke Historie); NSMT: National Science Museum, Tokyo; QM: Queensland Museum, Brisbane; RMNH: Collection numbers of NNM; SME: Station Marine d'Endoume, Marseille (most material will be deposited later in the Musée Nationale d'Histoire Naturelle, Paris); USNM: United States National Museum of Natural History, Washington DC; V.Pol: Polychaete collection numbers of ZMA; ZLU: Zoological Laboratory, Utrecht; ZMA: Zoologisch Museum, Instituut voor Taxonomische Zoölogie, Amsterdam; ZMH: Zoologisches Institut und Zoologisches Museum, Hamburg; ZMK: Zoologisk Museum, København.

TERMINOLOGY

The terminology used in this paper is explained in Figs 1 and 2.

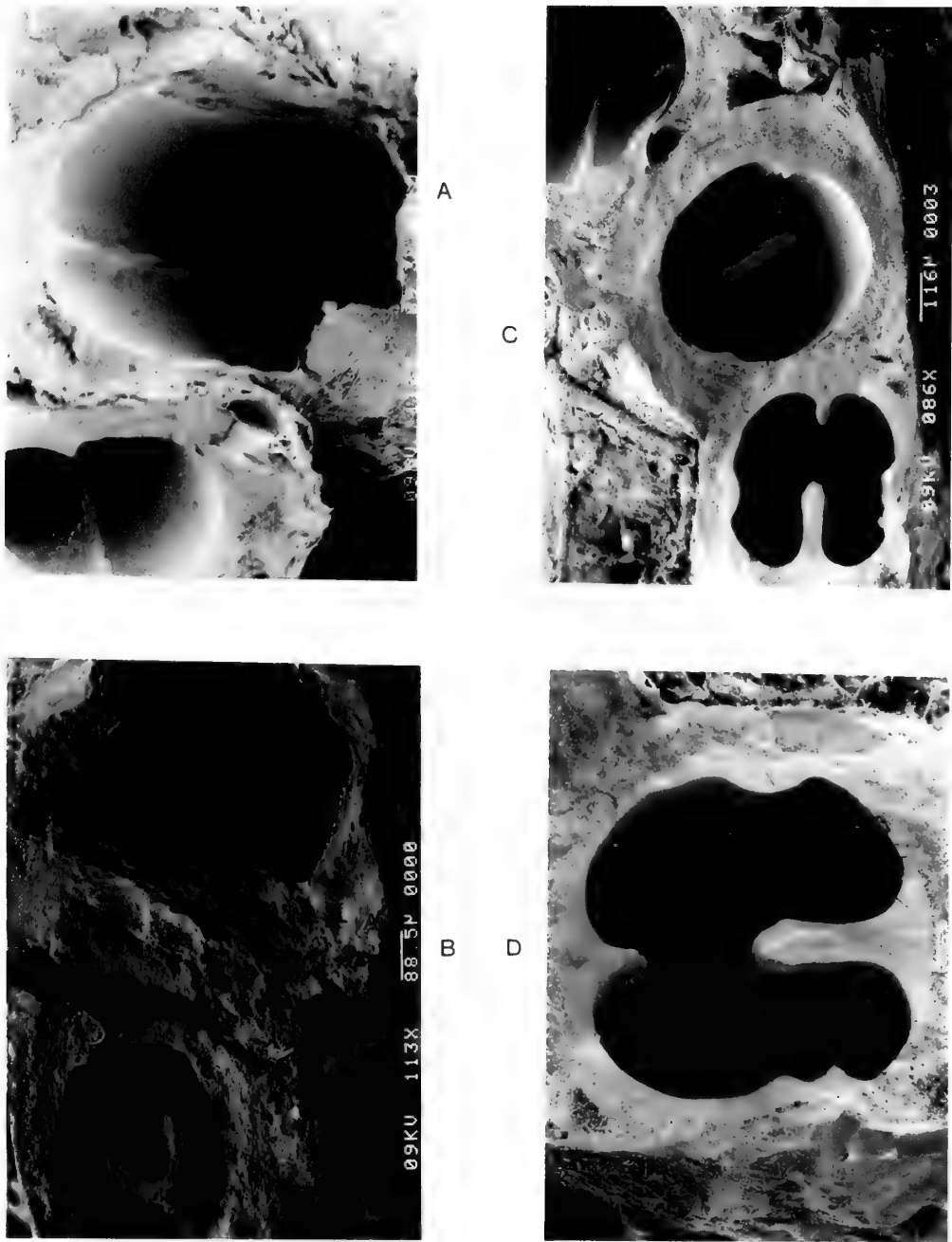


Plate 1 Scanning electron micrographs of fractured ends of tubes showing internal structures. A, C & D, *Spiraserpula lineatuba* (Straughan, 1967). B, *S. ypsilon* sp. nov.

DIAGRAMMATIC REPRESENTATIONS OF TUBES

The various arrangements of ITS in the species described are diagrammatically represented in Fig. 3.

DIAGNOSIS OF SPIRASERPULA Regenhardt, 1961

The original generic diagnosis of *Spiraserpula* was based only on the tube of its fossil type species, *S. Spiraserpula* Regenhardt, 1961. Pillai (1993) provides an emended definition for fossil species based on characters of the tube. However, the recent species described here are distinguishable not only by characters of their tubes but also of the worms themselves,

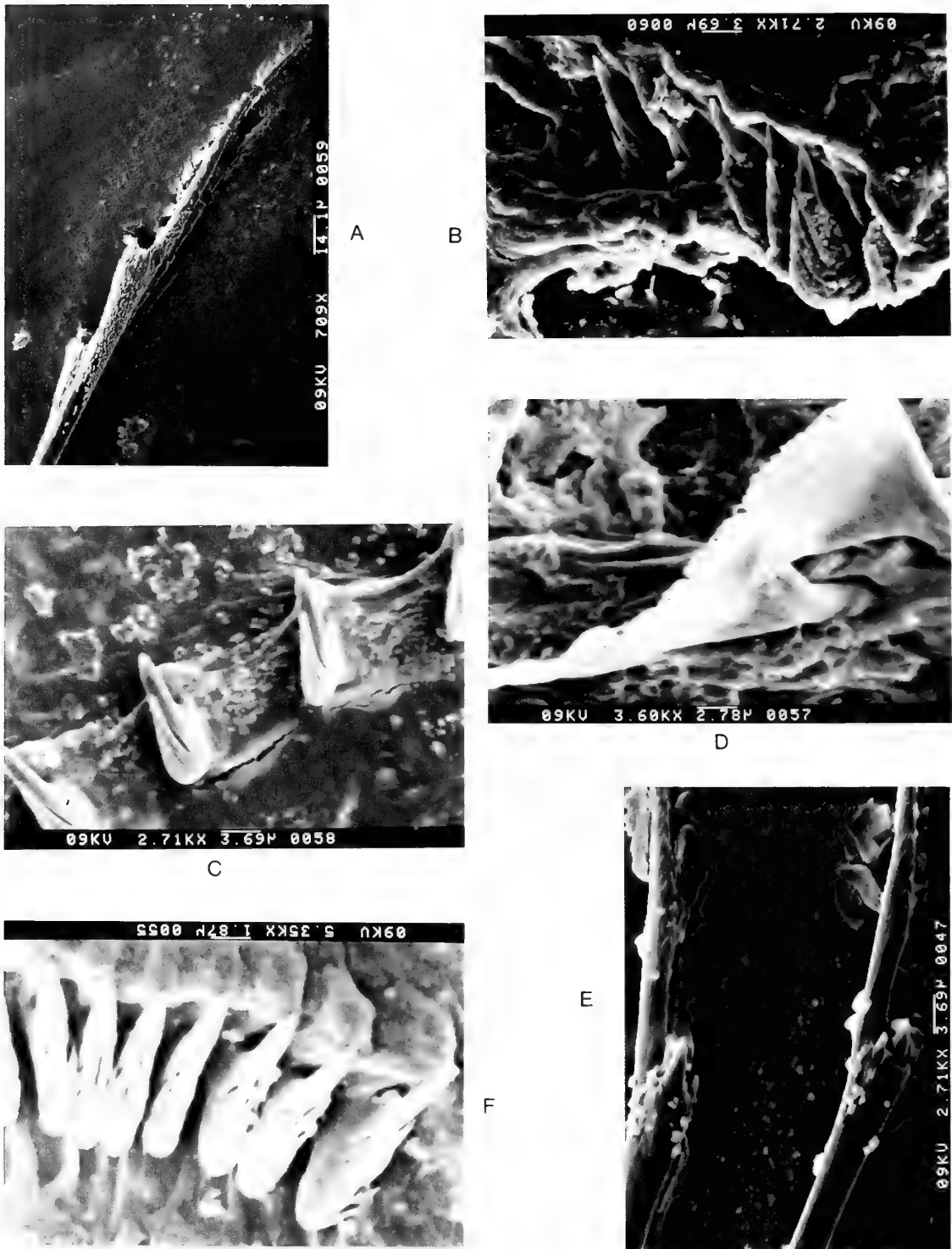


Plate 2 Scanning electron micrographs of chaetae. A–D, *Spiraserpula massiliensis* (Zibrowius, 1968): A, bayonet chaetae. B, thoracic uncini. C, anterior abdominal uncini. D, flat trumpet-shaped abdominal chaetae. E & F, *S. singularis* sp. nov.: E, bayonet chaetae. F, abdominal uncini.

and they have been taken into consideration in the following diagnosis:

Tube with internal structures, usually towards its earlier formed, coiled, posterior portions. They consist of internal longitudinal ridges which vary in form and complexity in the different species; they may be dorsal, along the convex inner

wall of the tube, and/or ventral, along the opposite side. They may be laminar, serrated or unserrated, or have other forms, and accessory lateral ridges or other structures may also be present. An umbilicus and peristomes may be present. There is usually an external granular overlay which bonds together coils of individual tubes, or those of other tubes to form

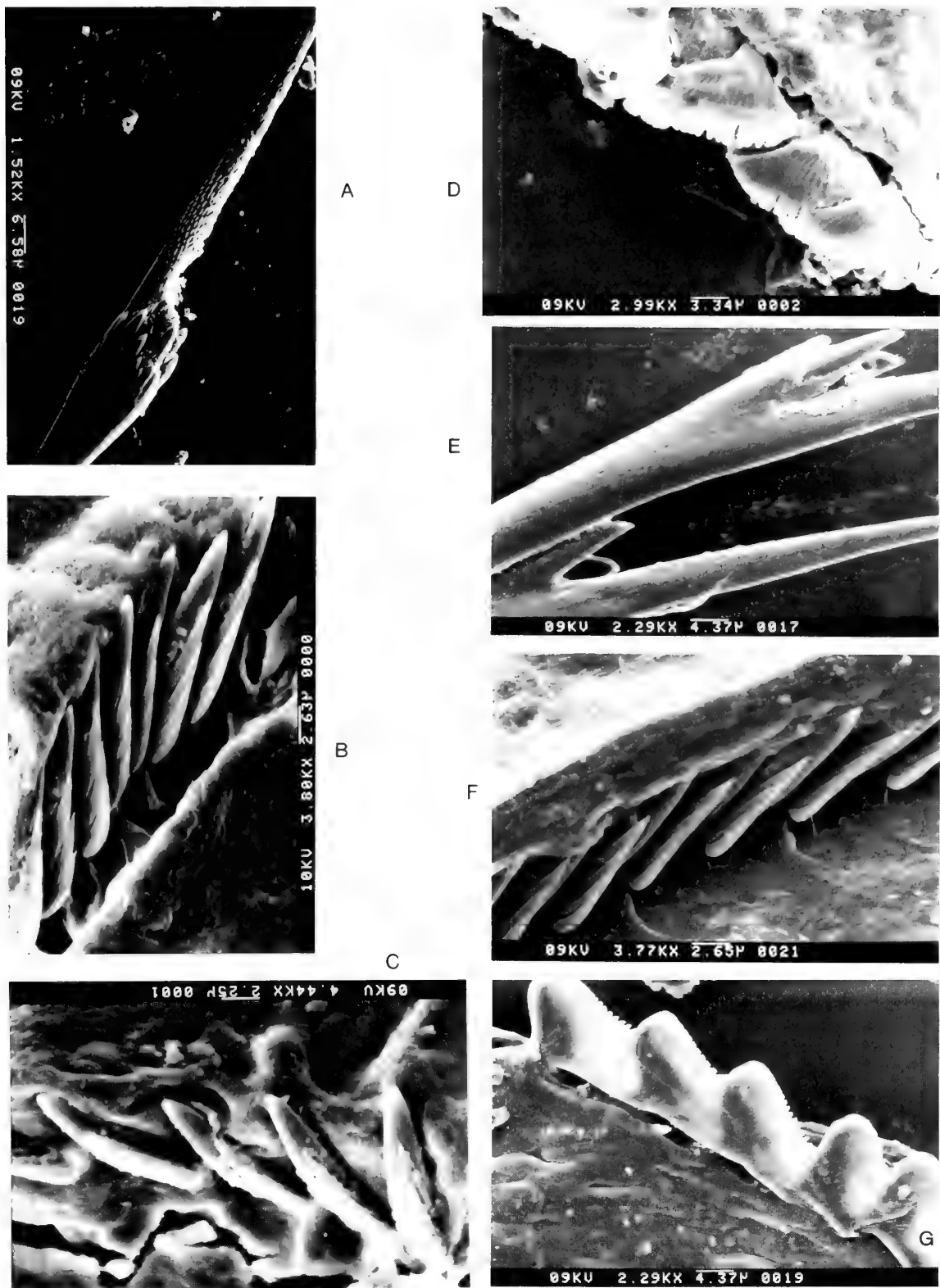
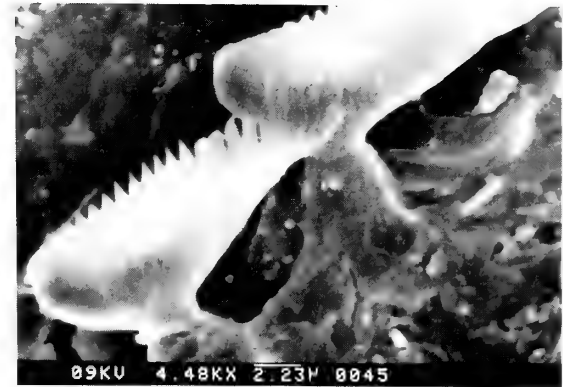


Plate 3 Scanning electron micrographs of chaetae. A–D, *Spirserpula nudicrista* sp. nov.: A, bayonet chaeta. B, thoracic uncini. C, abdominal uncini. D, flat trumpet-shaped abdominal chaetae. E–G, *S. lineatuba* (Straughan, 1967): E, bayonet chaetae. F, abdominal uncini. G, flat trumpet-shaped abdominal chaetae.



A



D



B



C



E

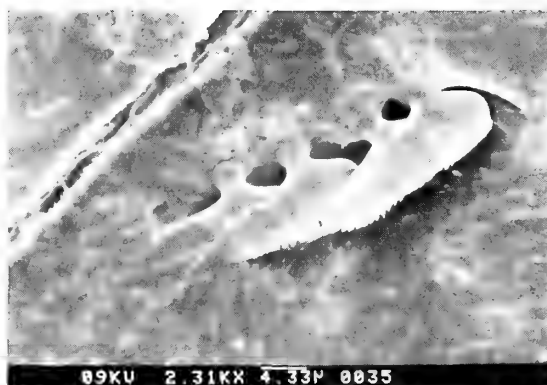


F

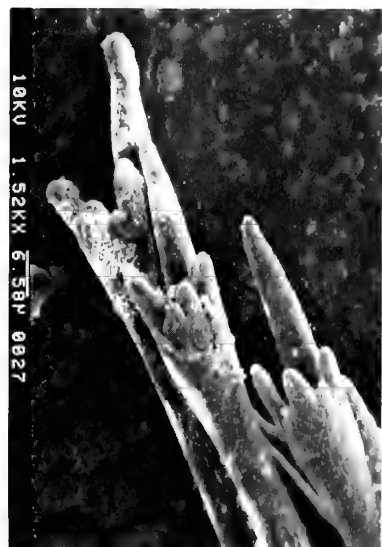
Plate 4 Scanning electron micrographs of chaetae. A–D, *Spiraserpula zibrowii* sp. nov.: A, bayonet chaetae. B, thoracic uncini. C, abdominal uncini. D, flat trumpet-shaped abdominal chaetae. E & F, *S. caribensis*, sp. nov.: bayonet chaetae.



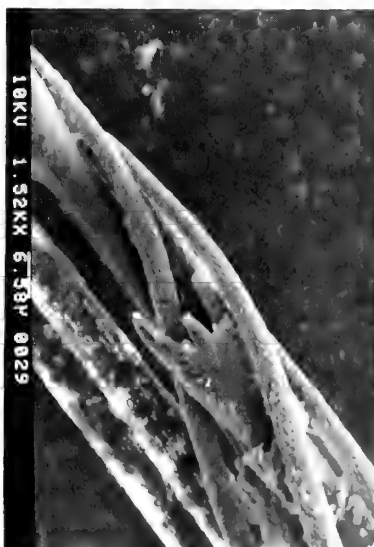
A



B



C



D



E



F



G



H

Plate 5 Scanning electron micrographs of chaetae. A–C, *Spiraserpula caribensis* sp. nov.: A, abdominal uncini. B, flat trumpet-shaped abdominal chaetae. C–E, collar chaetae from Grenada material. F–H, *S. snellii* sp. nov.: F, bayonet chaetae. G, abdominal uncini. H, flat trumpet-shaped abdominal chaetae.

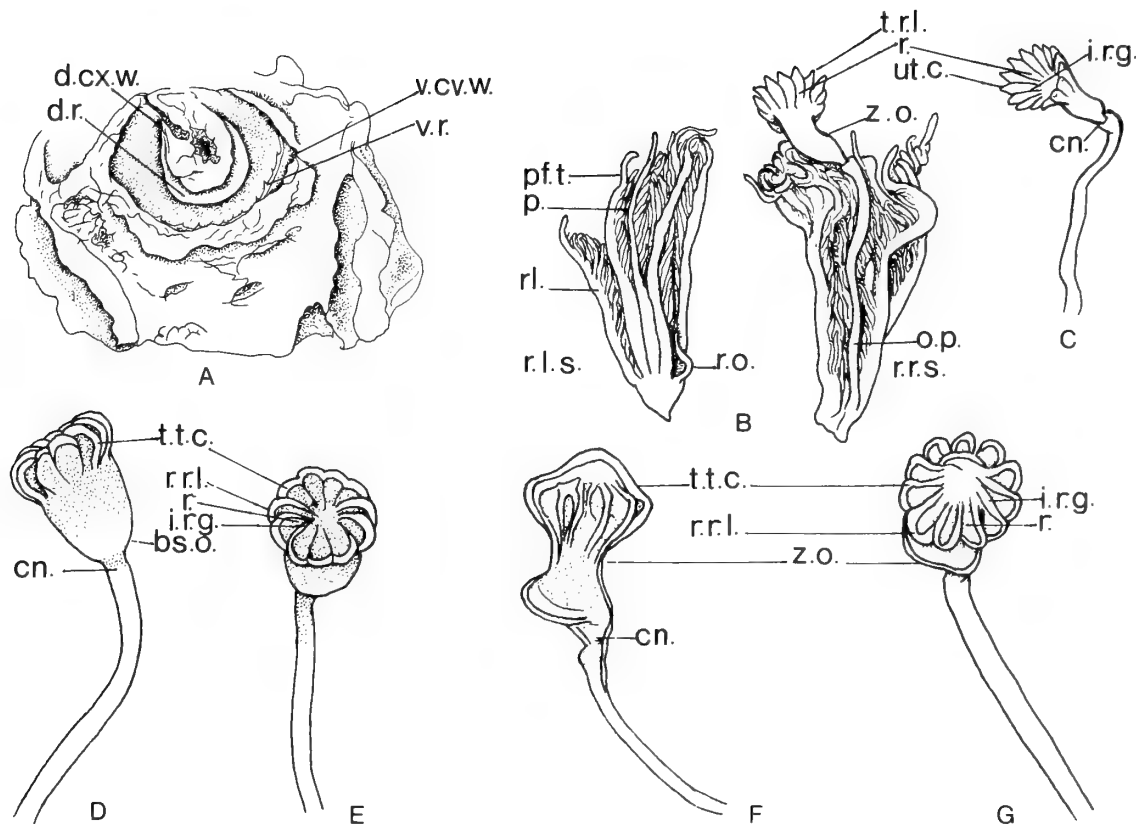


Fig. 1 Terminology. A, Tube: **d.cx.w.**, dorsal convex wall; **d.r.**, dorsal ridge; **v.cv.w.**, ventral concave wall; **v.r.**, ventral ridge. B, Radioles of both sides and operculum: **o.p.**, opercular peduncle; **p.**, pinnules; **pf.t.**, pinnule-free tip; **r.**, radius; **rl.**, radiole; **r.l.s.**, radioles of left side; **r.o.**, rudimentary operculum; **r.r.s.**, radioles of right side; **t.r.l.**, triangular radial lobe; **z.o.**, zygomorph operculum. C–G, Opercula: **cn.**, constriction between operculum and peduncle; **i.r.g.**, inter-radial groove; **ut.c.**, unthickened cuticle. **bs.o.**, bell-shaped operculum; **r.r.l.**, rounded radial lobe; **t.t.c.**, thickened transparent cuticle.

mutually bonded aggregations of a few to numerous individuals.

An operculum similar to that in *Serpula*, which is a modification of the second most dorsal radiole, is often present on one side with, correspondingly, a rudimentary operculum on the other. There may only be a rudimentary operculum on each side in certain species, while they may be present in juveniles and completely lost in older specimens in others. The shape of the fully developed operculum is characteristic for a particular species; it may be funnel-shaped, bell-shaped, zygomorphic or spherical. Its distal end may be concave or convex and usually bears radii which end as triangular or rounded lobes at the rim; but radii may also be lacking in some species. Its cuticle may be unthickened or thickened and transparent.

The number of branchial radioles is usually small, rarely up to 14 pairs. Palps absent. A pair of prostomial ocellar clusters is usually present. The number of thoracic chaetal tufts may exceed the seven pairs commonly occurring in many genera of Serpulidae, including *Serpula*, and those of the two sides are more frequently asymmetrical than symmetrical. Up to 14 have been counted on each side. Histological work is needed to ascertain the real extent of the segments, and their relation to numbers of chaetal tufts and uncinal rows, etc. The term 'chaetiger' is, therefore, used here in the literal meaning of 'hair bearer' and not as a synonym of segment. The thoracic

membranes end anterior to the last thoracic chaetigers, also more frequently asymmetrically than symmetrically. Unlike in most species of *Serpula sensu stricto*, therefore, a post-thoracic ventral flap (apron) is absent.

Collar fascicles bear chaetae of two kinds: bayonet chaetae and limbate chaetae, the blades of both of which are usually finely serrated. In the former, there are a few to several comparatively large teeth, located at the distal end of the shaft, separated from the bayonet-like blade by an unserrated area (unserrated notch). The range in the number of such teeth and the length of the unserrated notch varies in the different species. Limbate chaetae bear simple, more or less curved, blades. Thoracic and anterior abdominal uncini may bear teeth in a single row (saw-shaped), or are partly (saw- to rasp-shaped) or completely rasp-shaped. Abdominal chaetae bear distally flat trumpet-shaped ends, and are replaced by capillaries in the posterior segments. The distal ends of the abdominal chaetae of *Serpula* have been described as 'trumpet-shaped' in serpulid literature. We have discussed the inappropriateness of the comparison, as demonstrated by the scanning electron micrographs and drawings of these chaetae presented in this paper, and our attention has also been drawn to this by Zibrowius (pers. comm.). In order not to create confusion, it was decided to retain 'flat trumpet-shaped', for the present.

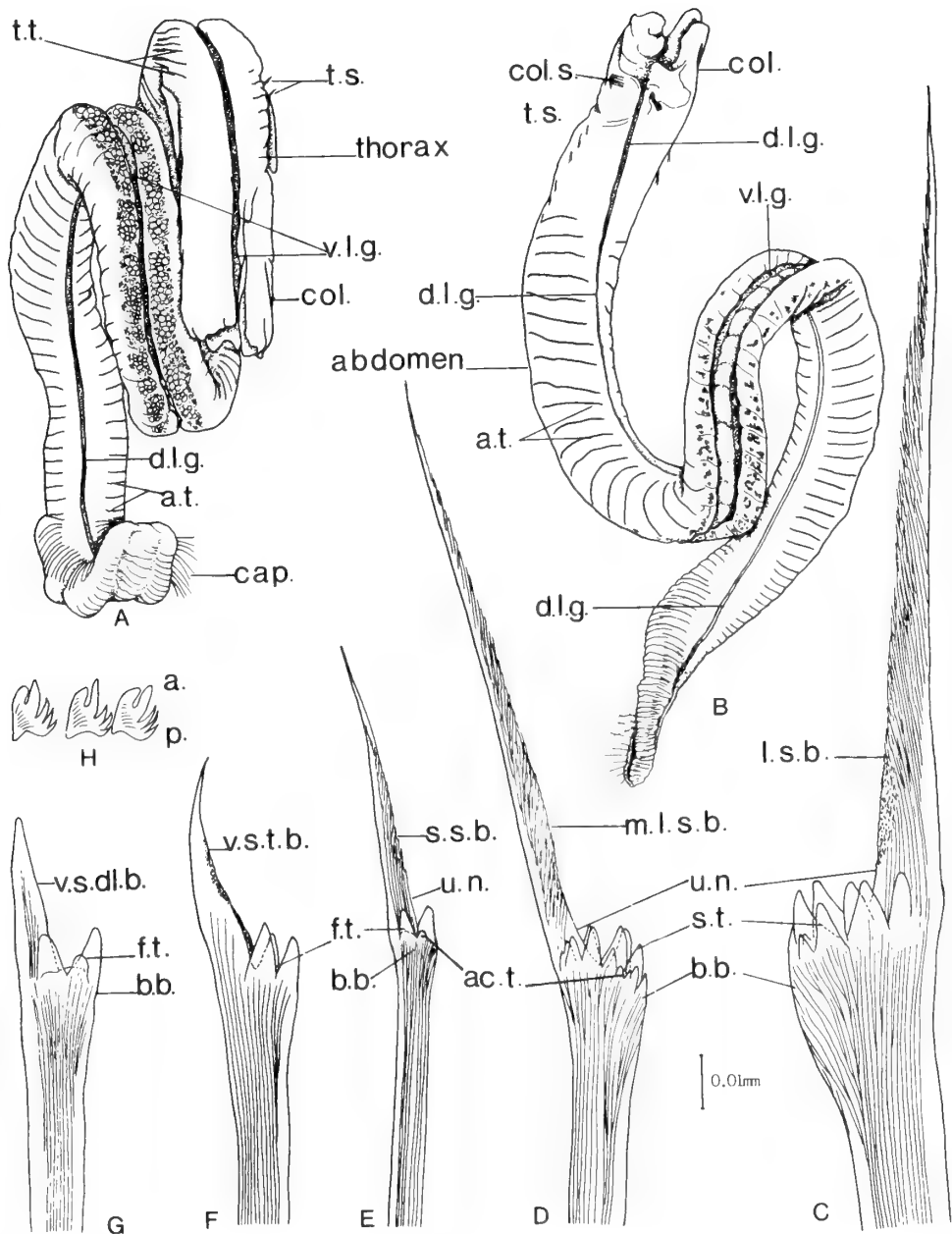


Fig. 2 Terminology. A & B, Body of worm: a.t., abdominal tori; cap., capillary chaetae; col., collar; col.s., collar chaetae; d.l.g., dorsal longitudinal groove; t.s., thoracic chaetae; t.t., thoracic tori; v.l.g., ventral longitudinal groove. C-G, Bayonet-shaped collar chaetae (after ten Hove & Jacobs, 1984; all same magnification): ac.t., accessory teeth; b.b., basal boss; f.t., few teeth; l.s.b., long serrated blade; m.l.s.b., moderately long serrated blade; s.s.b., short serrated blade; s.t., several teeth; u.n., unserrated notch; v.s.dl.b., very short dagger-like blade; v.s.t.b., very short tapered blade. H, Uncini, showing orientation in relation to the body of the worm: a., anterior; p., posterior.

**KEY TO THE KNOWN RECENT SPECIES OF
SPIRASERPULA REGENHARDT, 1961**

(See Figure 3 for terminology of ITS)

- 1. Tube with either dorsal or ventral internal longitudinal ridge only 2
- Tube with dorsal and ventral internal longitudinal ridges 7
- 2. Tube with dorsal longitudinal ridge only (Fig. 3, B-E) 3

- Tube with ventral longitudinal ridge only, exceptionally with few isolated teeth (Fig. 3, F) 6
- 3. Dorsal ridge unserrated, shaped like an inverted V (Fig. 3, B) *S. singularis* sp. nov. p.62
- Dorsal ridge serrated (Fig. 3, C-E) 4
- 4. Serrations of dorsal ridge deltoid (Fig. 3, C) *S. deltoides* sp. nov. p.80
- Serrations of dorsal ridge not deltoid (Fig. 3, D & E) 5

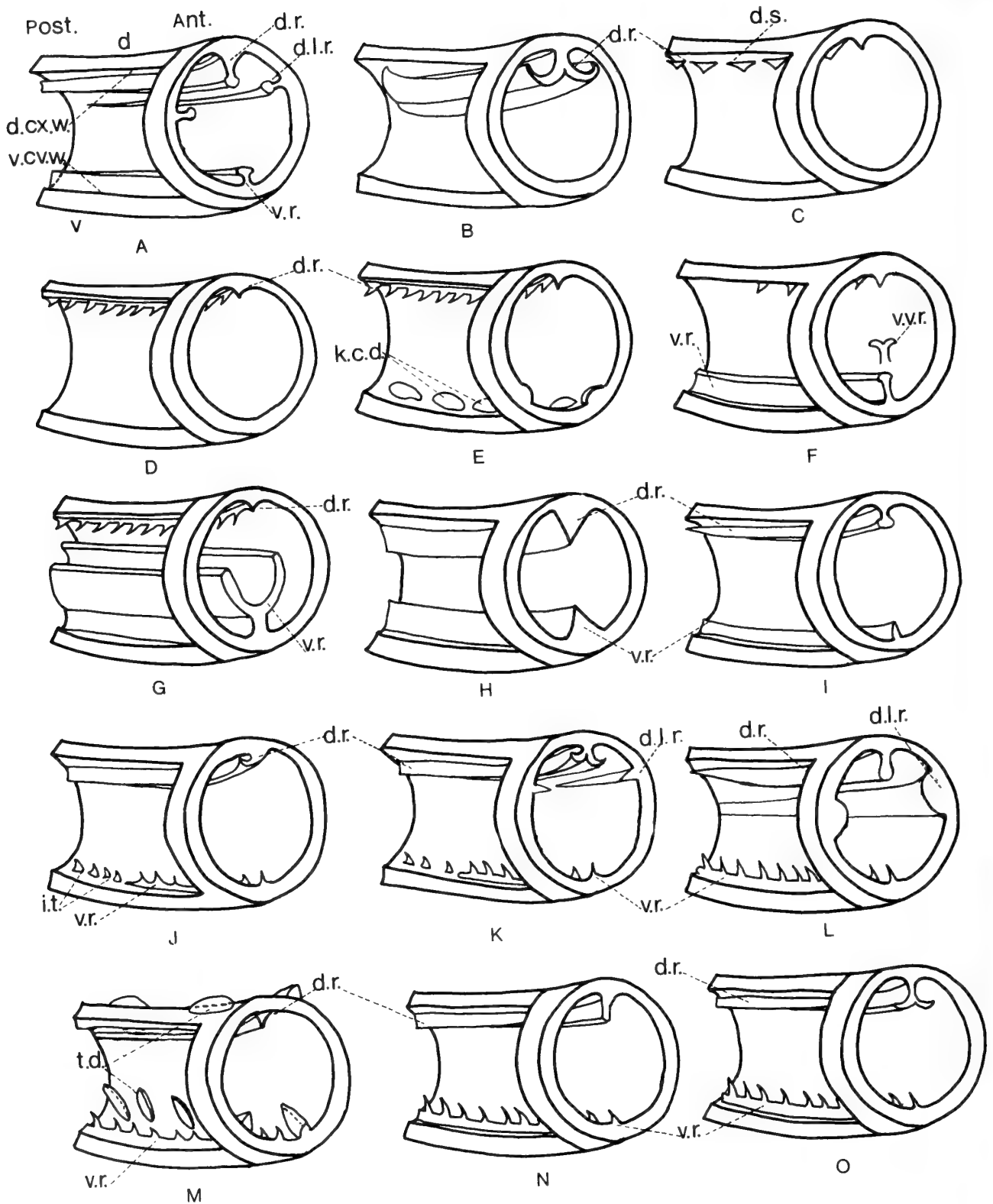


Fig. 3 Diagrammatic representations of ITS in the various species. A, Generalized drawing with all the main ITS. The orientation of the tube and terminology used are the same for all the diagrams. **Ant.**, anterior direction. **d.**, dorsal side. **d.cx.w.**, dorsal convex wall. **d.l.r.**, dorso-lateral ridge. **d.r.**, dorsal ridge. **v.**, ventral side. **v.cv.w.**, ventral concave wall. **v.r.**, ventral ridge. B, *S. singularis* sp. nov. C, *S. deltoides* sp. nov.; **d.s.**, deltoid serrations. D, *S. massiliensis* (Zibrowius, 1968). E, *S. capeverdensis* sp. nov.; **k.c.d.**, knob-like calcareous deposits. F, *S. nudicrista* sp. nov. & *S. snellii* sp. nov.; **v.v.r.**, variant form of ventral ridge. G, *S. ypsilon* sp. nov. & *S. paraypsilon* sp. nov. H, *S. sumbensis* sp. nov. I, *S. iugoconvexa* sp. nov. J, *S. vasseurii* sp. nov. K, *S. plaiae* sp. nov. L, *S. caribensis* sp. nov. & *S. lineatuba* (Straughan, 1967). M, *S. discifera* sp. nov.; **t.d.**, transparent discs. N, *S. karpatensis* sp. nov. & *S. minuta* (Straughan, 1967). O, *S. zibrowii* sp. nov.

5. Maximum number of radioles 6 pairs, abdominal segments about 50. Operculum may or may not be present. A shallow water species, down to about 60 m, rarely in deeper water *S. massiliensis* (Zibrowius, 1968) p.49
- Maximum number of radioles 8 pairs, abdominal segments about 145. Operculum absent. A deep water species occurring at depths of about 75–200m *S. capeverdensis* sp. nov. p.54
6. Tube creamish white, trapezoidal in cross-section. Operculum absent. Maximum number of radioles 9 pairs, pinnule-free tips very long. Prostomial ocelli prominently seen through collar. Unserrated notch of bayonet chaetae very short *S. nudicrista* sp. nov. p.76
- Tube mustard coloured, circular in cross-section. Operculum present. Maximum number of radioles 5 pairs, pinnule-free tips short. Prostomial ocelli not seen through collar. Unserrated notch of bayonet chaetae moderately long *S. snellii* sp. nov. p.84
7. Dorsal ridge serrated, ventral ridge Y-shaped (Fig. 3, G) ... 8
- Dorsal ridge unserrated, ventral ridge having other forms ... 9
8. Thoracic uncini without lateral tubercles. Maximum number of radioles 7 pairs, abdominal segments more than 100, about 130 *S. ypsilon* sp. nov. p.56
- Thoracic uncini with lateral tubercles. Maximum number of radioles 11 pairs, abdominal segments less than 100, about 90 *S. parapsilon* sp. nov. p.60
9. Ventral ridge unserrated (Fig. 3, I) 10
- Ventral ridge serrated (Fig. 3, J–O) 11
10. Tube white to faintly pinkish, circular in cross-section, external longitudinal ridges absent; dorsal and ventral internal longitudinal ridges pink, wedge-shaped in cross-section (Fig. 3, H). Operculum with up to about 21 triangular radial lobes, cuticle unthickened. Maximum number of radioles 5 pairs, abdominal segments below 100 (about 70); bayonet chaetae with several teeth on the basal boss *S. submensis* sp. nov. p.82
- Tube bright rose, quadrilateral to trapezoidal in cross-section, a pair of external longitudinal ridges, and a faint median one in places; dorsal and ventral internal longitudinal ridges white, dorsal ridge T-shaped in cross-section, ventral ridge very small (Fig. 3, I), may or may not be present. Operculum with up to about 12 rounded radial lobes, cuticle unthickened. Maximum number of radioles 14 pairs, abdominal segments over 100 (about 120); bayonet chaetae with two teeth on the basal boss *S. iugoconvexa* sp. nov. p.82
11. Bayonet chaetae with long blades and several teeth on the basal boss *S. vasseuri* sp. nov. p.78
- Bayonet chaetae with short to moderately long blades and few (2–7) teeth on the basal boss 12
12. Accessory lateral ridges present (Fig. 3, K & L) 13
- Accessory lateral ridges absent (Fig. 3, M–O) 15
13. Accessory ridges dorso-lateral. Dorsal ridge wedge- to Y-shaped in cross-section (Fig. 3, K), tube white *S. plaiæ* sp. nov. p.67
- Accessory ridges lateral. Dorsal ridge a simple plate, at most wedge to faintly T-shaped in cross-section (Fig. 3, L), tube pink or with pink longitudinal bands 14
14. Bayonet chaetae dagger-shaped, with short blunt blades. Operculum absent. Maximum number of radioles 6 pairs *S. caribensis* sp. nov. p.68

Bayonet chaetae with moderately long blades and tapering tips. Operculum present. Maximum number of radioles 5 pairs; *S. lineatuba* (Straughan, 1967) p.91

15. Tube with transparent discs attached to the wall externally and internally (Fig. 3, M) *S. discifera* sp. nov. p.94
- Tube without such discs (Fig. 3, N & O) 16
16. Operculum present *S. karpatensis* sp. nov. p.64
- Operculum absent 17
17. Bayonet chaetae with 5–7 teeth on basal boss; maximum number of radioles 4 pairs, abdominal segments about 55 *S. zibrowii* sp. nov. p.67
- Bayonet chaetae with 3–4 (rarely 5) teeth on basal boss; maximum number of radioles 6 pairs, abdominal segments about 80 *S. minuta* sp. nov. p.94

Although the ITS are very distinctive, the states of the characters need to be used with caution. In two species *S. lineatuba* (Straughan, 1967) and *S. caribensis* sp. nov., for example, 25–40 tube fragments had to be examined before the full extent of the development of dorsal and accessory ridges could be established; the latter are missing in most cross-sections. The shape of the distinctive inverted V, as in the dorsal ITS of *S. singularis* sp. nov. is only found in a small section in the earlier formed part of the tube; elsewhere, the ridge is a smooth plate only. Along this ridge, the rounded edge gradually becomes indented, gutter-shaped, and finally widening to form a V. This would apply to certain other characters as well. In *S. massiliensis* (Zibrowius, 1968) part of the sample from Marseille was operculate and part had rudimentary opercula only. However, all the specimens from a large sample from Portman had rudimentary opercula only. It may thus be expected that species which, on the basis of relatively few specimens, have been described as non-operculate, may turn out to be operculate when more material becomes available. As another example, two samples from Indonesia and Lizard Island (Queensland) initially appeared to belong to two distinct species, on the basis of differences in six character states. Additional material, however, yielded specimens with a full range of intermediate states, showing that they belong to one and the same species.

DESCRIPTION OF SPECIES

Spiraserpula massiliensis (Zibrowius, 1968) (Figs.4, A–O; 3, D; Pl.2, A–D)

SYNONYMY. *Serpula massiliensis* Zibrowius, 1968: 102–105, Pl.1, figs.24–37; Pl.14, fig.d.

Serpula massiliensis: Bianchi, 1981: pp.51–52, fig.16. *Serpula massiliensis*: ten Hove & Aarts, 1986: 35 [not the tropical E. Atlantic record, see *S. ypsilon*].

MATERIAL EXAMINED. Unless otherwise mentioned, the material was collected and/or determined by Zibrowius.

Mediterranean:

France: Marseille: 1. Anse des Cuivres; below SME, overhang 6m, 21.vii.1987 (10 out of several specimens, BMNH ZB 1989, 43–53). 2. Île Plane; submarine cave, 6m, legit G. Harmelin, vi.1987 (4 specimens, SME). 3. Île Plane; 1987 (5 out of several specimens, BMNH 1989 101–150). 4. Île Plane;

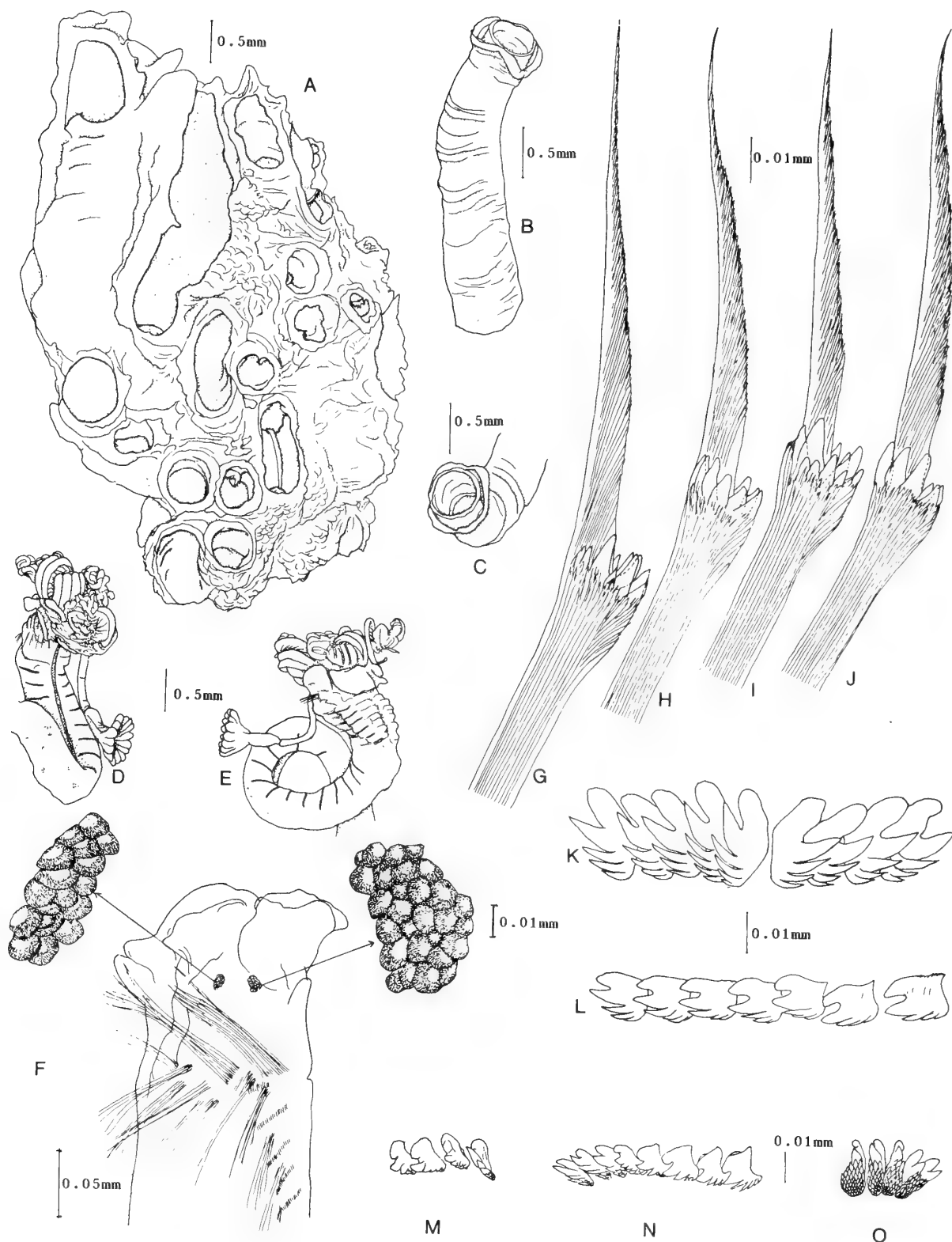


Fig. 4 *Spiraserpula massiliensis* (Zibrowius, 1968). A–O, From Marseille, Anse des Cuivres, BM(NH). ZB1989.43–53. A, Aggregation of tubes with fractured ends showing the serrated dorsal ridge along the convex inner wall, and granular overlay. B–C, Erect parts of tube with four-lobed peristome. D, Anterior part of operculate worm. E, Same specimen showing end of thoracic membrane. F, Thorax with pair of prostomial ocellar clusters, also enlarged. G–J, Four bayonet chaetae from the same fascicle. K, Row of thoracic uncini. L, Anterior abdominal uncini. M & N, Middle abdominal uncini. O, Posterior abdominal uncini.

submarine cave, 6m, legit G. Harmelin, vii.1971 (7 specimens, ZMA V. Pol.3159). 5. Friocil Harbour (5 out of several specimens, BMNH ZB 1989 54–100). 6. Grand Conglu; 1987 (5 out of several specimens, BMNH ZB 1989 151–200). 7. Martigues; ca. 50km W of Marseille, Ponteau Electric Plant, under stones, 1.3m, 5.iv.1977 (2 out of several specimens, SME). 8. La Ciotat; ca 30km E. of Marseille, Bec de l'Aigle, on concretions of sand, 40m, iii.1970 (3 specimens, SME). 9. Canyon de la Cassidaigne; about 20km E of Marseille, off Cassis, from 170–270m by dredging, 15.vi.1974 (tubes, 1 specimen, SME).

NW Corsica: 10. Revellata, 15m, calcareous algal masses, 8.iv.1978 (2 specimens, SME).

Italy: 11. S coast of Sorrento peninsula, 'Grotto Zaffiro', 10m, 29.v.1974 (3 specimens, SME). 12. Bari; 10m, cave, legit T.M.Griessinger, 8.vii.1968 (5 specimens, SME).

Greece: 13. Gulf of Corinth, Aspra Spitia, 5m, 26.ix.1977 (3 specimens, SME).

Malta: 14. Oxford University Underwater Exploration Group 1965, scrapings from roof of cave, det. Pillai (2 specimens, BMNH ZB1989 32–36).

Tunisia: 15. Tabarka; algal concretions, 31–36m, 24.iv.1969 (1 specimen, SME). 16. Zembra Islands, concretions, 35m, 30.iv.1969 (few tubes with portions of worms, SME). 17. 'Dauphin' Stn.24, 35°12'N 11°25'E, 73m, on Arca, legit Bane, Medit. Mar. Sorting Center, 28.viii.1967 (1 specimen, SME). 18. Gulf of Gabes; 'Calypso', 34°05'N 10°48'E, 23m, muddy sand with *Caulerpa* meadow, on shelly material, 20.iv.1965 (1 specimen, SME1887). 19. Gulf of Gabes; 'Calypso', 34°13'N 10°31.9'E, 31m, *Caulerpa* meadow, 27.iv.1965 (1 specimen, SME 1910).

SE Spain: 20. Cabo de Palos; ca 50km E of Cartagena, 6m, legit A. Ramos, 4.iv.1982 (3 specimens, SME). 21. Portman; 20km E of Cartagena, small overhang, 0.5–1.0m, on rock covered by dark brown sediment, the latter retained on the tube surfaces by oil pollution, 5.iv.1984 (20 out of several specimens, SME).

Portugal: 22. From a submarine cave near Sagres, Algarve, legit H. Zibrowius Sept. 1986 (BMNH) 1992. 181–255).

NE Atlantic: 23. Gorrige Bank; 'Meteor' M9c, Stn.95, AT 29, 36°29.9'N 11°33.0'W, 150–430m, 24.vi.1967 (some empty tubes, SME). 24. Madeira Archipelago; Jean Charcot, Stn.42, SW of Porto Santo, approx. 33°0.4'N 16°24.5'W, 125–145m, 17.vii.1966 (empty tubes, information pers. comm. H.Zibrowius). 25. Canary Islands; W coast of Palma, Tijarafe, 28°42'N 17°58'W, 20m, CANCAP 4.D14, det. M. Aarts (5 out of several specimens, RMNH 18465, ZMA V.Pol.3739, BM(NH) 175–180). 26. NW Africa; off Point Elbow, ex Spanish Sahara, 'Tenace' D16, Stn. 23, 24°13'N 16°17'W, 50–60m, legit Marche-Marchard, 13.iv.1967 (4 specimens, SME).

TYPE LOCALITY. Marseille (France).

DESCRIPTION. In order to follow the variations within the genus *Spiraserpula* it was considered useful to have as complete a description as possible of one member of the group, *S. massiliensis* was selected because of the large amount of material available from various sources. The following updated species description is based on the original account as well as additional data obtained from a study of the above collections, which include much of Zibrowius' original material.

According to Zibrowius (1968), the tubes are white, circu-

lar in cross-section and, although difficult to measure because of their coiling, may attain a length of 50.0 mm for a diameter of about 0.5–1.0 mm. Their coiling is highly irregular and the direction may reverse. Sometimes many tubes are joined together, coiling in the same direction. They are relatively thick, except in their erect portions which are cylindrical. At intervals along the latter, there may be one to a few outwardly directed expansions, generally referred to as peristomes. They are sometimes in the form of four, somewhat symmetrically placed lobes. In dense populations, the erect tubes may form a kind of uniform meadow in submarine caves of the Mediterranean (Zibrowius, pers. comm.). The surface of the tube is covered by faint granulations which, very rarely, may form short longitudinal ridges.

It is difficult to remove the worms from their tubes. When removed, quite a number of specimens lacked their radiolar crowns. An operculum may be present or absent. When absent there is a rudimentary operculum on each side. When present, the operculum is small, and its diameter does not correspond with that of the tube. Its distal end is flattened to slightly funnel-shaped, bearing 13 to 23 obtuse lobes. The peduncle is more slender than the pinnulate radioles, and its attachment to the operculum is central and constricted. The corresponding radiole of the opposite side is reduced to a filamentous rudimentary operculum, about one-third the length of the radioles, and lacks pinnules.

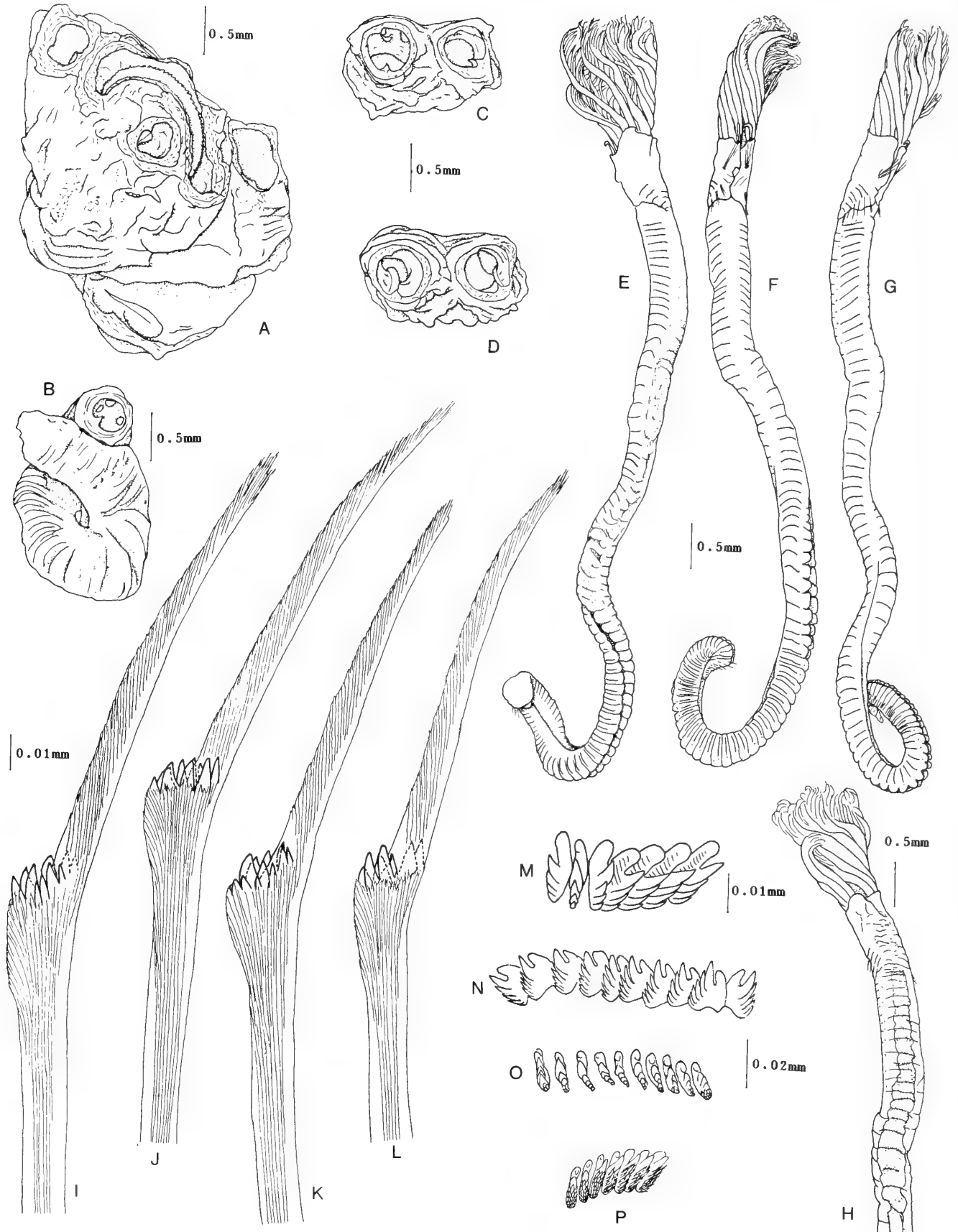
The collar consists of a large ventro-medial lobe and a smaller one on either side of it, all of which are rounded. The thoracic membranes are broad and well developed up to about the fourth thoracic chaetiger, and reduced posteriorly. They are not united to form a post-thoracic ventral flap or apron. The number of thoracic segments may exceed the usual seven found in many other species of *Serpula*. Each collar fascicle generally possesses four bayonet-shaped chaetae and a similar number of simple bladed chaetae. Each bayonet chaeta has a striated blade distally, and several teeth on the basal boss. Thoracic uncini bear 3–5 teeth. Anterior abdominal bundles consist of 2–3 flat trumpet shaped chaetae. Uncini possess 2–5 teeth in a single row. The posterior abdominal segments bear long capillary chaetae, and rasp-shaped uncini with several rows of teeth.

Additional data obtained during the present study are as follows:

TUBES: White to faintly creamish, and may occur in closely intertwined masses of a few to several individuals (Fig. 4, A); sometimes solitary. Except for their free erect portions, they are mutually bonded to various extents, particularly at their bases. Their 'granular overlay' is shown in Fig. 4 A, and the four-lobed peristomes in Fig. 4, B & C.

An important character which had not been reported relates to the tube, which bears ITS. In its first formed portion, which is normally coiled, there is a serrated longitudinal ridge. Careful removal of numerous specimens from their tubes has shown that this serrated ridge is always on the convex side of the coils, as also found in masses consisting of several individuals (Fig. 4, A). The orientation of the worm within the tube is such that the posterior dorsal part of its abdomen is always applied to this serrated 'dorsal ridge' (Fig. 3, D). This, in addition to its tight coiling, accounts for the difficulties encountered in extracting complete worms from their tubes by Zibrowius (1968) and in the present study.

The numerous specimens in the collection from Portman show an apparent exception in lacking ITS. However, confir-



mation that the specimens belong to this species came from a very small number of old and empty tubes at the bottom of the aggregations having the characteristic serrated internal dorsal ridge. The population had been subjected to oil pollution, as evidenced by a thick deposit of it which covered the tubes externally, and even lined them thinly internally.

WORMS: The longest operculate specimen (from Île Plane, Marseille, BMNH ZB 1989 101–150) is 19.0 mm long; its thoracic width 1.1 mm. It has 5 pairs of radioles, in addition to an operculum on one side and a rudimentary operculum on the other. It also has the longest operculum and peduncle, 3.5 mm; its operculum is 1.0 mm long, 1.2 mm in diameter, bell-shaped, and with 11 rounded marginal lobes. The abdomen is 13.5 mm long and has 51 segments, the last four with capillaries. The longest non-operculate specimen, from the same locality, has a total length of 20.0 mm. Its abdomen is 15.5 mm long and has 43 segments, the last ten with capillaries. The two specimens indicate variations in abdominal length due to extent of contraction during fixation, and that the number of segments in the abdomen may not be always proportional to its length. In the other specimens studied, the length of the operculum together with the stalk ranges from 1.0–2.0 mm; the operculum from 0.5–0.6 mm in length and 0.3–1.5 mm in diameter.

The shape of the operculum varies from an elongate funnel in the majority of cases to a narrow bell in the others (Fig. 4, D, E). The opercular radii end in 10–16 rounded marginal lobes. The width of the peduncle, just before the constriction, is 3/5ths to 4/5ths that of the proximal end of the operculum. The number of radioles observed is 4–6 pairs, and their pinnule-free tips vary in length from 1/5th to 2/3rd the total length of the radiole (i.e. radiole plus pinnule-free filament). Zibrowius (1968) reported a higher maximum number of up to 23 marginal lobes on the operculum. This high number, in one specimen, is apparently not representative of the species (Zibrowius, pers. comm.).

A total of 67 specimens from different localities (including 21 from the abnormal Portman material, *vide* below) were examined for various characters. All the Portman specimens possess only rudimentary opercula. Out of 46 specimens from the other collections 25 possess an operculum, 12 lack one, and the rest are indeterminate since they lack radiolar crowns. The majority of specimens from normal populations, therefore, possess an operculum.

Another character, hitherto not reported, is the presence of two light red to reddish-brown clusters of prostomial ocelli (Fig. 4, F). They can be seen when a worm with its radioles removed is viewed from the anterior end, or through the collar in mounted specimens. Each ocellus consists of a pigmented cup-shaped part, and a transparent anteriorly or antero-laterally directed lens-shaped part within it (Fig. 4, F). Thoracic glands, as found in other species of the genus, are absent.

The numbers of thoracic chaetal tufts, 6 to 9 on each side, may be symmetrical or asymmetrical. The condition in 26

Table 1 *Spiraserpula massiliensis* (Zibrowius). Number of thoracic chaetal tufts on each side.

No. of individuals (n=26)	1	4	7	11	3
No. of thoracic chaetal tufts	6/7	7/7	7/8	8/8	8/9

Table 2 *Spiraserpula massiliensis* (Zibrowius). Extent of the thoracic membranes of the two sides.

No. of individuals (n=21)	1	2	10	2	3	3
Thoracic membrane ends	4/5	4/6	5/5	5/6	6/6	6/7

specimens is summarized in Table 1. Likewise, the thoracic membranes may end symmetrically or asymmetrically, but always anterior to the last thoracic chaetiger; an apron is, therefore, absent (Fig. 4, E). The condition in 21 specimens is given in Table 2.

Collar fascicles bear 3 to 5 bayonet chaetae each. Bayonet chaetae consist of a long serrated blade, an unserrated notch of moderate length, and a basal boss with several teeth of variable size (Fig. 3, G–J; Pl. 2, A). Thoracic and anterior abdominal uncini usually have 4 or 5 teeth arranged in a single row (edge saw-shaped), (Fig. 4, K, L; Pl. 2, B & C). In the intermediate abdominal region, the edge of each uncinus is saw-shaped anteriorly whereas several teeth are placed side by side (edge rasp-shaped) posteriorly. The number of teeth in a single row decreases and the rasp-shaped posterior portion increases as the posterior end of the abdomen is reached (Fig. 4, M–O). Although the posterior abdominal uncini are rasp-shaped, they have a single large tooth anteriorly (Fig. 4, O).

LIVE MATERIAL. (*Vide* Zibrowius, 1968)

HABITAT AND DISTRIBUTION. This species is commonly found in submarine caves and at depths accessible by diving (Zibrowius, 1968). The original description mentioned a depth of 10–22m, but subsequently the species was found to occur in shallower and deeper water (see list of material examined). Deeper water collections came from depths of 31–36m (Tunisia) and 58–60m (off Point Elbow, Western Sahara), the latter consisting of operculate and non-operculate specimens. Empty tubes of this and other serpulid species typical of shallow water have been obtained along the steep slope of the Goringe Bank at 150–430m. This occurrence may be due to slumping from shallower depths (Zibrowius, pers. comm.). The Madeira Archipelago material (125–145m) also consisted of dead material. The empty tubes and single specimen from Canyon de la Cassidaigne (170–200m) is also exceptional. In general, therefore, the species commonly occurs in depths to about 60m, rarely down to about 200m.

S. massiliensis is common in the Mediterranean (Greece,

Fig. 5 *Spiraserpula capeverdensis* sp. nov. A–P, From type locality (SW of São Vicente), CANCAP 6.148 & 6.146; A–L, From 6.148, M–P, from 6.146. A, Opened tube showing serrated internal dorsal ridge along the convex wall of coiled part; and granular overlay in places. B, Coiled part of tube with fine transverse growth wrinkles externally, and its fractured end showing dorsal ridge on convex inner wall, and two ventro-lateral longitudinal rows of smooth tubercles on opposite wall. C & D, Cross-section of two tubes, both with serrated internal dorsal ridge, and one with ventro-lateral rows of tubercles. E–G, Three views of same worm showing rudimentary opercula (F), condition of the thoracic membranes (G), and dorsal longitudinal groove (E & G), and ventral abdominal groove posteriorly (E). H, Anterior end of younger specimen. I–L, Bayonet collar chaetae, all from same fascicle. M, Thoracic uncini. N, Anterior abdominal uncini. O, Uncini from transitional region of abdomen. P, Posterior abdominal uncini.

Italy, France, Spain, Malta, and Tunisia). In the eastern Atlantic it is abundant in submarine caves, and has been recognized on Gorringe Bank, the Madeira Archipelago, Portugal and the coast of Sahara.

S. massiliensis has been erroneously reported from the Red Sea (Amoureux *et al.*, 1978). Examination of the specimens (HUJ) showed that their tubes lack ITS and they do not, therefore, belong to the genus *Spiraserpula*.

***Spiraserpula capeverdensis* sp. nov.**

(Figs.5, A–P; 3, E)

MATERIAL EXAMINED.

Cape Verde Islands: All CANCAP stations. **Off São Vicente:** 1. 6.134; 110–120m, (2 PARATYPES and some empty tubes, RMNH 18197). 2. 6.135; 110–150m, (1 PARATYPE, BM(NH) 1992.8). 3. 6.137; 75–90m, (1 PARATYPE, BM(NH) 1992.9). 4. 6.146; 75m, (1 specimen, BMNH). 5. 6.148; 100–200m, (HOLOTYPE, 2 PARATYPES & 3 empty tubes (residual material) ZMA VPol. 3651). 6. 6.166; 78–85m, (1 PARATYPE, USNM 130995). **Off Razo:** 7. 7.117, 100–120m, (some empty tubes, RMNH 18198). 8. 7.123; 120m, (5 specimens, RMNH 18199, ZMA V.Pol.3733). **Scuba diving station : Boa Vista:** 9. 7.D06; down to 12m, (3 questionable specimens, ZMA V.Pol. 3871).

TYPE LOCALITY. Cape Verde Islands, São Vicente.

DESCRIPTION.

TUBES: White, nearly circular in cross-section, and occurring in aggregations of a few individuals, occasionally solitary. They are closely coiled amongst or upon themselves (Fig. 5, A), and mutually bonded by a granular overlay. Erect portions, when present, are very short, hardly rising above the rest of the tube, and may end in four lobes. Faint growth rings are sometimes present (Fig. 5, B), and anterior uncoiled portions may sometimes show a few transverse thickenings, representing peristomes. In their first formed parts, they possess an internal serrated dorsal ridge (Fig. 5, A, D) and, often, a short ventro-lateral longitudinal row of small smooth knob-shaped processes on each side (Figs.5, B, C; 3, E). A mid-dorsal longitudinal groove in the posterior part of the abdomen (Fig. 5, E, G) is applied to the serrated dorsal ridge when the worm is withdrawn into the tube. The maximum external diameter of the tube varies from 0.6 mm in a juvenile to 1.4 mm in older specimens.

WORMS: (Fig. 5, E–H). An operculum is absent in all the specimens examined. Instead, a filamentous rudimentary operculum is present on each side. The number of radioles in the larger specimens is often 7 or 8 per side, 4 in the smallest. They are about 2.0 mm long in the larger specimens, and have transverse specks at intervals. Their pinnule-free tips are slender, 1/5 to 1/6 the total length of the radioles. Two

Table 3 *S. capeverdensis* sp. nov. Measurements and meristic data.

Stn. No.	TL (mm)	Width of thorax (mm)	No. of radiol.	Length of abdom. (mm)	No. of abdom. segs.	Caps. on
6.137	25.9	0.5	8/8	22.7	138	27
6.148	20.6	0.5	7/8	17.5	145	—
6.148	7.1	0.5	7/8	6.9	96	12
7.123	2.9	0.3	4/4	2.6	49	—
7.123	2.4	0.3	4/4	2.2	29	9

Table 4 *S. capeverdensis* sp. nov. Numbers of thoracic chaetal tufts and extent of thoracic membranes.

No. examined (n=12)	2	1	2	1	4	2
No. of thoracic chaetal tufts	9/8	8/8	8/7	8/5	7/7	7/6
No. examined (n=9)	1	4	2	2		
Thoracic membrane ends	6/6	5/5	5/?	4/4		

clusters of reddish to reddish-brown prostomial ocelli are present.

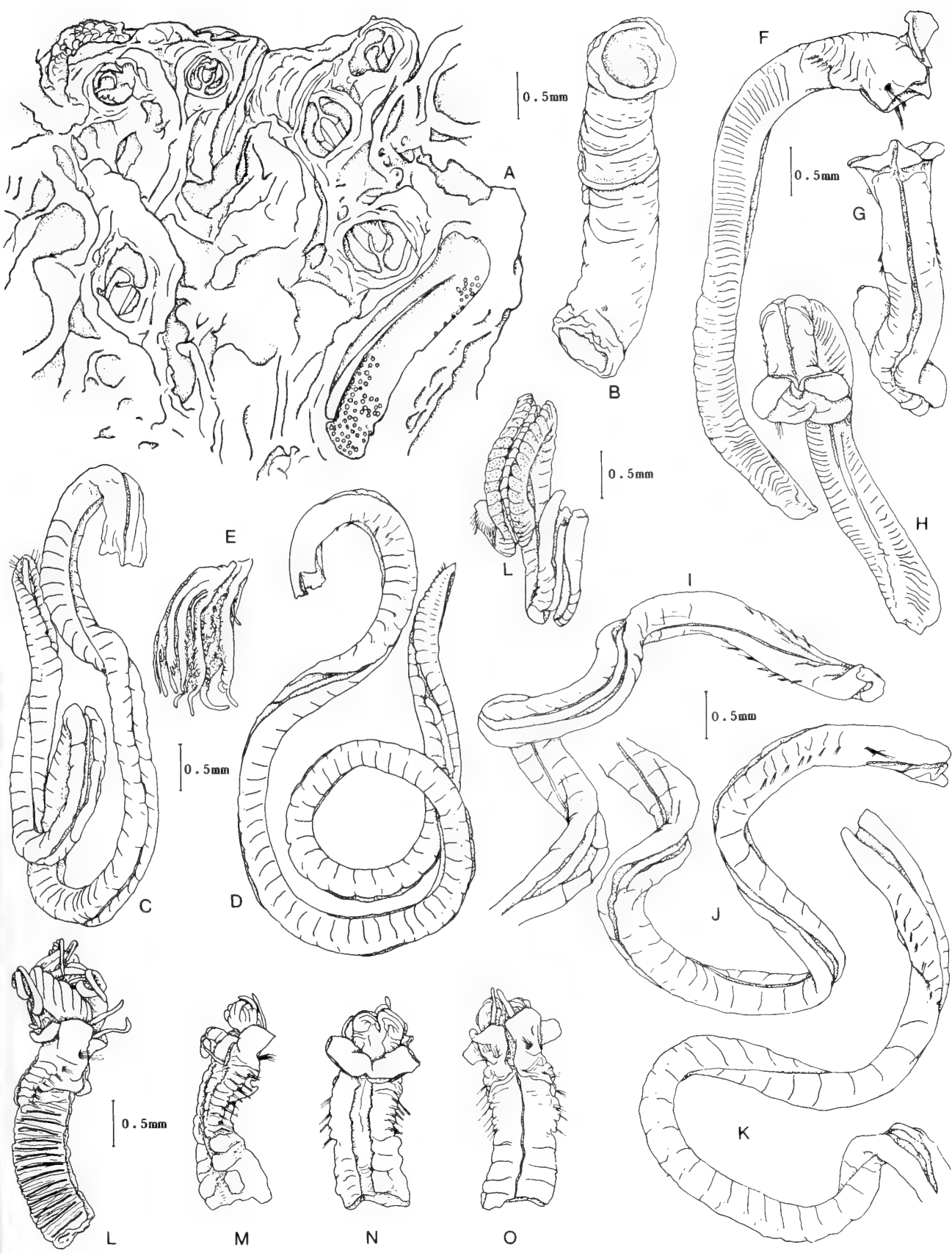
Measurements and other data from the two longest and three juvenile worms are presented in Table 3. The numbers of thoracic chaetal tufts and the extent of the thoracic membranes on the two sides is variable, as shown in Table 4.

The thoracic membranes do not extend to the last thoracic chaetigers (Fig. 5, F), and apparently end symmetrically, but further study of additional material is necessary for confirmation of the latter. Ventral thoracic glands are absent.

Each collar fascicle bears up to about 5 bayonet chaetae (Fig. 5, I–L). They have a long serrated blade, a short unserrated notch and several moderately large teeth on the basal boss. Thoracic uncini (Fig. 5, M) usually have 4 teeth in a single row. Anterior abdominal uncini are similar, with 4–6 teeth (Fig. 5, N). The posterior abdominal uncini are rasp-shaped, except for the single anterior tooth (Fig. 5, P). There is a transition (Fig. 5, O) between the condition found in the anterior and posterior abdominal uncini.

The differences between *S. capeverdensis* sp. nov. and *S. massiliensis* are as follows: The former has only rudimentary opercula, and higher maximum numbers of radioles (8 pairs) and abdominal segments (145). Its tubes do not form tall erect portions, and usually possess two ventro-lateral rows of knob-shaped tubercles internally, in addition to the serrated dorsal ridge. In *S. massiliensis*, however, an operculum may or may not be present, the maximum number of radioles is 6 per side, and of abdominal segments observed 51. There is also strong indication of an ecological difference (see below).

Fig. 6 *Spiraserpula ypsilon* sp. nov. From type locality material (SW coast of Island of Brava), CANCAP 6.D03. A, Aggregation of fractured tubes showing ITS, consisting of a Y-shaped ventral ridge along the concave wall and a serrated dorsal ridge along the convex wall. An oblique section (bottom right) shows the tapering anterior end of the ventral ridge. B, Erect portion of tube showing four-lobed peristome. C–E, Different views of complete worm showing rudimentary opercula, pinnule-free tips of the radioles (E), and dorsal and ventral longitudinal abdominal grooves. F–H, Same anterior end showing four-lobed collar (H), thoracic chaetigers and membrane (F), and ventral longitudinal groove. I–K, Three views of larger specimen, showing dorsal and ventral longitudinal abdominal grooves. Note the longitudinal cord-shaped structure within the ventral groove of the abdomen which fits into the gutter-shaped part of the Y-shaped ventral ridge of the tube. L, Anterior portion of worm accidentally fixed outside its tube, showing filamentous rudimentary opercula and thoracic membranes. M–O, Three views of anterior part of another worm fixed outside its tube. Its thorax is considerably wider than those of specimens fixed within their tubes, and the longitudinal grooves may be stretched and shallow (N).



REMARKS. Although the few damaged specimens from Stn. 7.D06 are very similar to *S. capeverdensis* in most respects, only 2 tube parts (out of 10 recognizable fragments) showed a serrated dorsal ridge and possibly latero-ventral knobs. As opposed to all material of *S. capeverdensis* studied so far, a specimen in a tube without visible internal structures showed a bell-shaped operculum with 13 radii. Therefore the identification of this lot is left at ? *capeverdensis*.

LIVE MATERIAL. No records.

ETYMOLOGY. Named after the type locality.

HABITAT AND DISTRIBUTION. *S. capeverdensis* sp. nov. is known only from the Cape Verde Islands, mainly from depths of 75–200m where the bottom consists of various combinations of coarse sand, shell gravel, calcareous stones, calcareous nodules, calcareous algae and sponges, on which it occurs among the epifauna.

Scuba diving to 15–20m, in a total of 28 different stations off the Cape Verde Islands during CANCAP–VI and CANCAP–VII, did not yield this species from the shallower coastal waters. However, the dives yielded a different species, *S. ypsilon* sp. nov., from these depths which, in the Mediterranean, are typical for *S. massiliensis*.

***Spiraserpula ypsilon* sp. nov.**

Figs. 6, A–K; 7, A–T; 34, G; Pl. 1, B)

SYNONYMY. *Serpula massiliensis*: ten Hove & Aarts, 1986: 35 (tropical E. Atlantic record only).

MATERIAL EXAMINED.

Cape Verde Islands: CANCAP stations. **Scuba diving stations:** 1. 6.D01; S coast of **São Tiago**, SE of Porto Praia, 15m (1 specimen, RMNH 18177). 2. 6.D02; S coast of **São Tiago**, Baía de Santa Clara, 20m, caves in rock (2 out of several specimens; RMNH 18187; BM(NH) 1992.85–115; FSBC I 39197 (1); AM W 20339 (1); NSMT (1)). 3. 6.D03; SW coast of **Brava**, Porto dos Ferreiros, 15m (30 specimens: HOLOTYPE & 5 PARATYPES, RMNH 18176. Other PARATYPES: ZMA V. Pol. 3650 (10); USNM 130993 (6) and BM(NH) 1992.73–82 (10)). 4. 6.D06; SW coast of **São Nicolau**, Baía do Tarrafal, 15m (4 specimens, RMNH 18188). 5. 6.D10; S. coast of **São Vicente**, 15m (5 out of several specimens, RMNH 18189). **Coastal stations:** 6. 6.K13; SW coast of **Ilha Razo**, (14 out of several specimens, RMNH 18190, ZMA V. Pol. 3726, USNM). 7. 6.K15; SW coast of **Ilha de Santa Luzia**, (1 out of several specimens; bulk RMNH 18191; clusters of 10–15 tubes each BM(NH), 1992.116–120; ZMA V. Pol. 3727; HUJ; Dr M. Jäger). 8. 6.K21; NE coast of **São Vicente**, Baía das Gatas, (3 specimens, RMNH 18192). **Scuba diving stations:** 9. 7.D03; **Cima**, SE coast, (1 specimen, RMNH 18193). 10. 7.D05; **Maio**, SW coast of Ponta Preta (2 out of few specimens, RMNH 18194). 11. 7.D06; **Boa Vista**, Ilhéu de Sal Rei, 12m (1 out of few specimens, ZMA V. Pol. 3728). 12. 7.D10; **Razo**, S coast, 20m (1 out of few specimens RMNH 18195; BM(NH) 1992. 121–131; ZMH). **Dredging station:** 13. 6.148; off **São Vicente**, 100–200m (1 empty eroded tube; RMNH 18196). **Tropical Western Atlantic, Gulf of Mexico:** 14. Florida, Stn. EJ66–460, 26°24'N

82°28'W, 18m, 6.xii.1966, 'Hourglass' Stn J, (20 out of several specimens, FSBC I, ZMA V. Pol. 3729, BM(NH) 1992. 132–147). 15. Florida: Stn. EJ 67–76, 27°37'N 83°28'W, 39m, 2.iii.1967, 'Hourglass' Stn. C, (few specimens, FSBC I, ZMA V. Pol. 3730). 16. Florida: Stn. EJ67–328, 27°37'N 83°07'W, 18m, 11.ix.1967, 'Hourglass' Stn. B (4 out of several specimens, ZMA V. Pol. 3731). **Caribbean:** 17. **Aruba:** Andicuri, cape W of beach, windward side, rockpool, exuberant coral growth, strong wave action, 0.5m, legit H.A. ten Hove, 28.viii.1970, Stn. 2034B (together with *S. caribensis* sp. nov.; ZMA V. Pol. 3732). 18. **Colombia:** Santa Marta area, Cabo and Ojo del Aguja, 8–27m, legit J. W. Dulfer and M. J. C. Rozenmeyer 1986, ident. as *S. massiliensis* (1 damaged specimen, tube; ZMA V. Pol. 3778). **Bermuda:** 19. Stn. 14, legit Reed, with a note by Zibrowius in 1970 indicating that it is a new species (3 specimens, USNM 43244).

TYPE LOCALITY. Cape Verde Islands, Brava.

DESCRIPTION.

TUBES: Faintly pinkish, often with a more pronounced shade of light pink or light mauve in the granular overlay towards their anterior ends. They normally occur in mutually bonded highly coiled aggregations, occasionally also singly, adjacent to the aggregations. The granular overlay is fine, somewhat translucent and nearly uniform (partly shown in the top left portion of Fig. 6, A). External longitudinal ridges are normally absent, but up to three may be faintly developed on the less coiled tubes of solitary specimens. Their anterior portions are generally attached, often with their lateral borders extending somewhat over the substratum. Occasionally, they possess erect ends which attain an external diameter of up to 1.25mm, and may bear a few peristomes which are usually four-lobed and outwardly directed (Fig. 6, B).

The ITS are more complicated than those of the other known species of the genus, with the exception of the closely related species *S. parapsylon* sp. nov. As seen in carefully opened tubes or through their fractured ends in an aggregation (Fig. 6, A), they consist of a serrated dorsal ridge, and a thin, very fragile, Y-shaped ventral ridge (Fig. 3, G; Pl. 1, B). The gutter-shaped part and the stem of the latter gradually decrease anteriorly until they are represented only by a simple ventral ridge, which itself decreases in height and gradually disappears (Fig. 6, A, bottom right corner). These ridges commence in the first formed portions of the tube, but usually extend more anteriorly than in most of the other species of the genus. The inner translucent layer of the tube is faintly pinkish, as is the Y-shaped ventral ridge. In addition, the latter may possess one or two thin dark pink longitudinal stripes on the outside of the gutter-shaped part, one along the top and the other along the bottom.

WORMS: Some measurements and counts are provided in Table 5–8.

The worms attain a total length of about 27.5mm, a thoracic width of 0.6mm, a maximum of about 131 abdominal segments, with capillaries on the last 10 segments or so. The maximum number of radioles is 8 pairs. The two specimens with 4 pairs of radioles are juveniles. The pinnule-free tips are short to moderately long, up to about 1/5 the entire length

Fig. 7 *Spiraserpula ypsilon* sp. nov. A–O, From type locality, CANCAP 6.D03. P–T, From Florida Stn. EJ 66–460. A–E, Bayonet chaetae from same fascicle. F–I, Same, from second specimen. J, Thoracic uncini. K, Uncini from first abdominal torus. L, Uncini from third abdominal torus. M, Anterior abdominal uncini from another specimen. N, Uncini from mid-abdominal torus (transitional region). O, Posterior abdominal uncini. P–T, Bayonet chaetae of one fascicle.

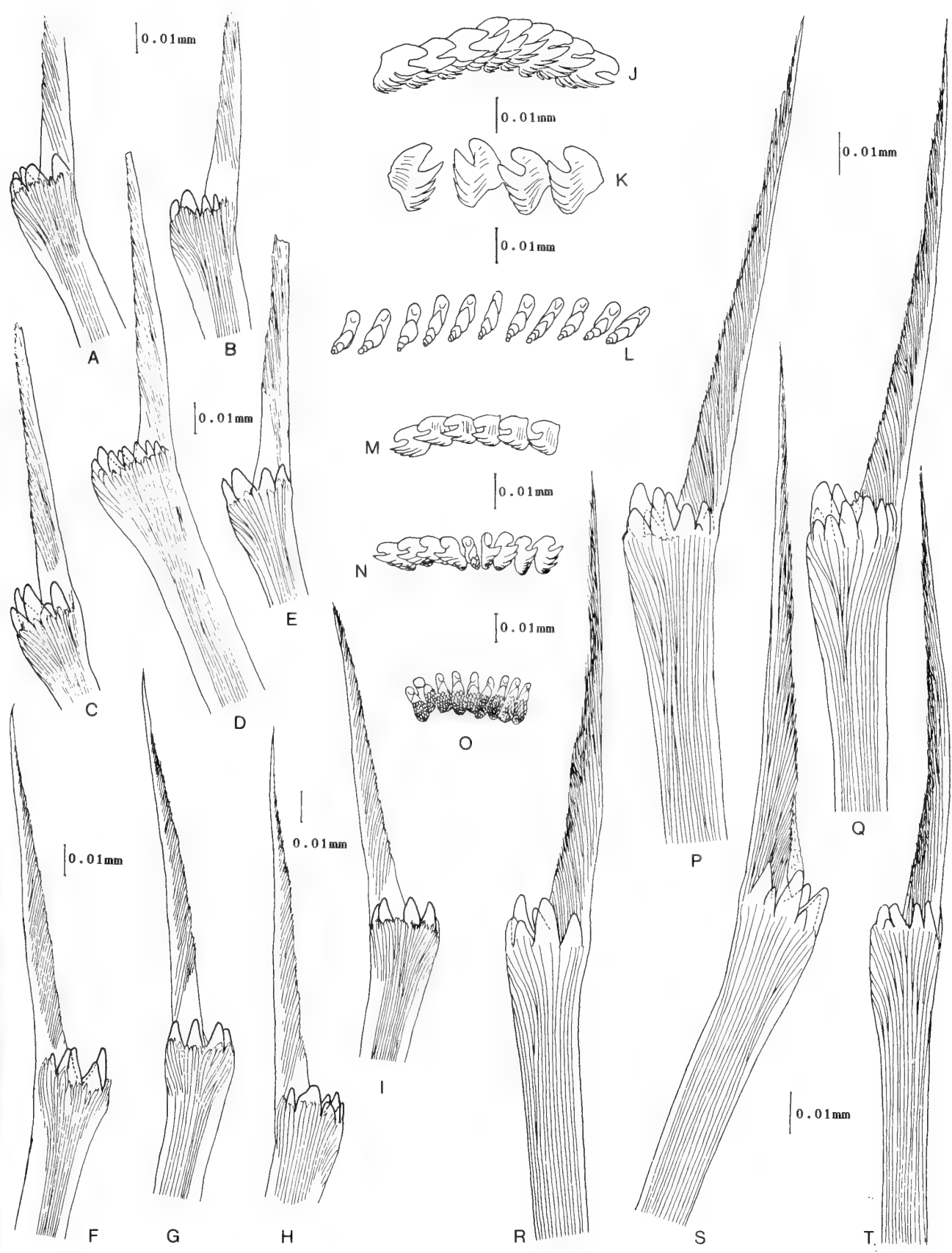


Table 5 *S. ypsilon* sp. nov. Measurements (mm) and counts.

Total length	27.5	15.6	14.1	11.7	6.3	6.0	4.6
Thoracic width	—	0.6	0.6	0.4	0.5	0.5	0.4
No. of radioles	—	7/7	8/8	5/5	6/6	6/6	4/4
Abdominal length	25.5	11.0	11.3	8.5	4.6	4.3	2.6
No. of abdom. segs.	113	88	131	107	37	57	37
Capillaries from	103	80	124	99	24	44	30

Table 6 *S. ypsilon* sp. nov. Numbers of radioles.

No. of specimens (n=37)	1	6	15	13	2
No. of radioles (L/R)	8/8	7/7	6/6	5/5	4/4

Table 7 *S. ypsilon* sp. nov. Numbers of thoracic chaetal tufts in 69 specimens.

No. of specim.	1	2	1	9	2	2	16	23	3	8	1	1
Nos. of tufts.	10/9	10/8	9/9	9/8	9/7	9/6	8/8	8/7	8/6	7/7	7/6	7/5

Table 8 *S. ypsilon* sp. nov. Extent of thoracic membranes in 43 specimens.

Number of specimens	5	31	6	1
Thor. membranes end on	6/6	6/5	5/4	5/3

of the radioles (Fig. 6, E). Live material from Stns. 7.D03 and 7.D05 showed a pair of pigmented ocelli at the base of each radiole, externally. An operculum is absent; there is a filamentous rudimentary operculum on each side (Fig. 6, E, L, O).

Two clusters of reddish to reddish-brown prostomial ocelli are present. Although the width of the thorax ranges from 0.4–0.6 mm in specimens preserved within their tubes, it can be wider in anterior portions of worms accidentally preserved outside their tubes (Fig. 6, F–H, L–O). The median lobe of the collar is sub-rectangular, rounded laterally and with a smooth mid-ventral notch, giving the entire collar a four-lobed appearance (Fig. 6, F–H & L–O).

The numbers of thoracic chaetal tufts on the two sides range from 5 to 10, and may be symmetrical or asymmetrical, as are the endings of the thoracic membranes (Tables 7 & 8). Paired thoracic glands are absent.

Collar fascicles bear up to about four fully developed bayonet chaetae and two more being formed deep within the fascicle, with a similar number of simple bladed chaetae. Juveniles possess fewer, often two fully developed bayonets and two more being formed within the fascicle. Each bayonet chaeta has a long serrated blade, a short unserrated notch, and few to several moderately large somewhat conical teeth with smooth tips on its basal boss (Fig. 7, A–E, F–I). The serrations of the blade are short towards its proximal part,

Table 9 *S. ypsilon* sp. nov. from Florida (EJ– 66–460).

Measurements and meristic data from two longest specimens out of 22 measured.

	Total length (mm)	Thoracic width (mm)	No. of radioles	Abdomen Length (mm)	No. of segs.	Caps from
Specimen 1	22.7	0.6	7/7	18.5	110	97
Specimen 2	20.7	0.8	6/6	16.7	130	111

Table 10 Meristic and other data on *S. ypsilon* sp. nov. from Florida (EJ– 66–460).

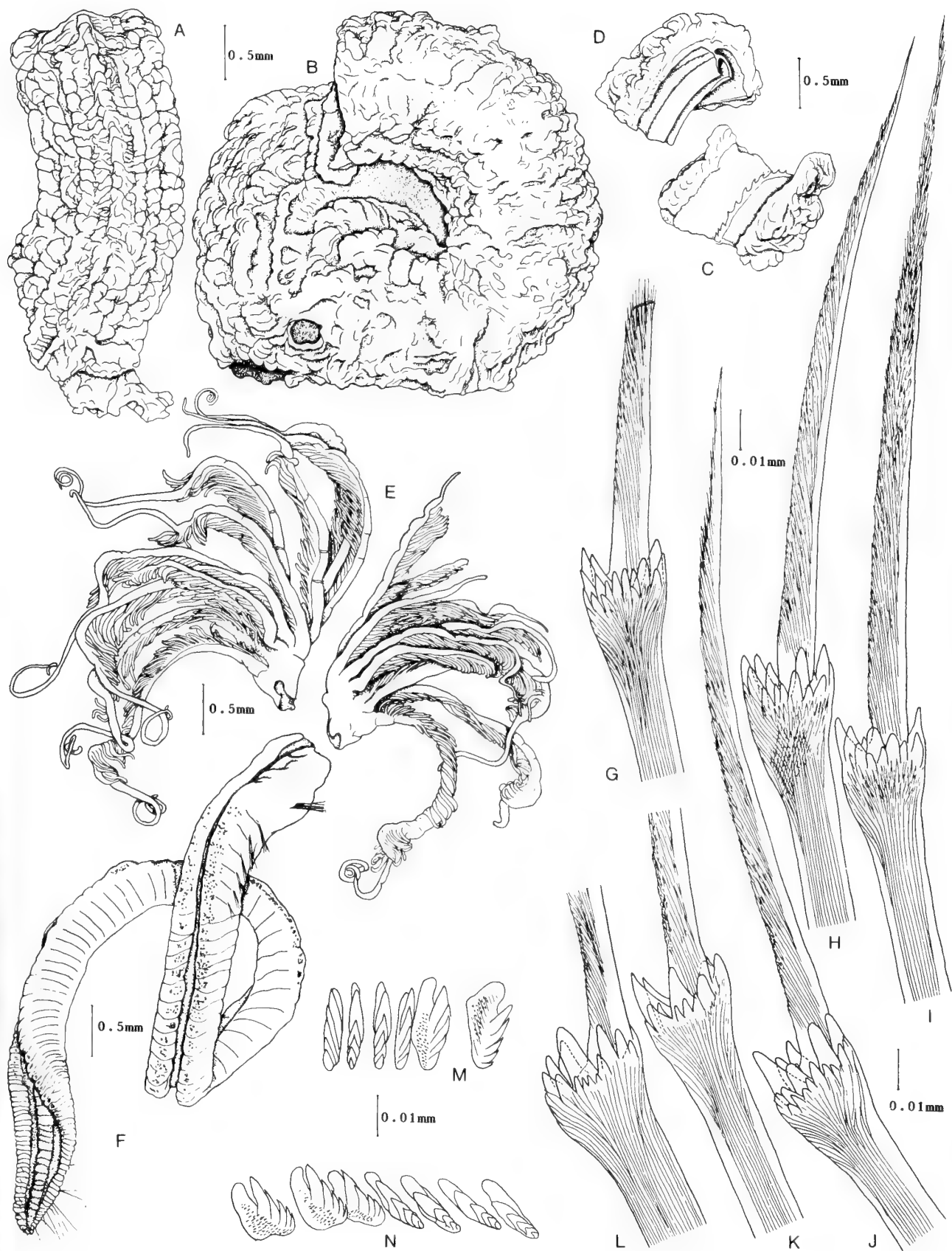
No. of specimens (n = 14)	4	2	4	1	2	1			
No. of radioles	7/7	7/6	6/6	6/5	5/5	3/5			
No. of specim. (n = 29)	1	1	1	4	6	9	4	2	1
No. of th. chaetal tufts	10/9	10/7	9/9	9/8	8/8	8/7	7/7	7/6	7/5
No. of specimens (n = 20)	1	1	10	7	1				
Thor. membrane ends	7/5	6/5	5/5	5/4	4/4				

but somewhat pilose distally. Thoracic uncini are mostly with 6 teeth, but some have 4 or 5 (Fig. 7, J). Anteriorly there are up to 4 flat trumpet chaetae in each bundle, posteriorly there are 1 or two capillaries instead. Anterior abdominal uncini usually have 4 or 5 teeth arranged in a single row (Fig. 7, K–M). The posterior abdominal uncini are rasp-shaped, with a single anterior tooth and several (4–6) rows of teeth posterior to it (Fig. 7, O). In between, there is a progressive reduction in the number of teeth in a single row, and a corresponding increase in the rasp-shaped area (Fig. 7, N). The special adaptations of the body of the worm in relation to the internal structures of the tube are as follows: A narrow longitudinal groove extends along the mid-dorsal line of the abdomen and thorax (Fig. 6, C, D, H–K, O). The abdomen and thorax are also grooved ventrally, and within this longitudinal groove, forms a cord-shaped longitudinal ridge (Fig. 6, C, D, I–L). The orientation of the worms within their highly coiled tubes is such that the dorsal groove is applied to the serrated dorsal ridge of the tube, and the cord-shaped ventral abdominal ridge fits into the gutter-shaped part of the Y-shaped ventral ridge of the tube. The latter, in turn, fits into the ventral groove of the body.

COLLECTIONS FROM THE WESTERN ATLANTIC. *S. ypsilon* has also been collected from Florida, Bermuda and Aruba.

Study of material from Florida (EJ– 66–460) provided the following data: The external diameter of the tubes attains 1.1 mm. A granular overlay is present. The external colouration varies from faintly creamish to faintly pinkish. Their internal colouration and structures are similar to those from

Fig. 8 *Spiraserpula parapsylon* sp. nov. A, Tube from Curaçao, NA, Cornelisbaai, showing granular overlay and longitudinal ridges. B–N, From Klein Bonaire Stn. 2105A. B, Tube with indistinct longitudinal ridges. C–N, From holotype. C, Tube fragment showing serrated dorsal ridge along convex wall. D, Tube fragment with Y-shaped ventral ridge along opposite wall. E & F, Adult worm; E, Radioles of both sides, with very long pinnule-free tips and lacking rudimentary opercula. F, Body showing dorsal and ventral longitudinal abdominal grooves and ventral pigment patches. G–L, Bayonet collar chaetae. M, Thoracic uncini of holotype showing lateral denticles. N, Anterior abdominal uncini, with more prominent denticles.



the Cape Verde Islands. The colouration of the worms in alcohol shows a difference. The radioles and body have an overall fleshy to dark reddish-brown colour, with blackish pigment clusters ventro-laterally in the abdominal segments. Whether this colour difference is due to different methods of fixation or not needs to be verified. Maximum sizes encountered have been given in Table 9.

An operculum is absent, but a pair of rudimentary opercula is present. Up to 10 thoracic chaetal tufts per side were counted, and the extent of the thoracic membranes is variable, however, never reaching the last thoracic chaetiger. Meristic and other data are given in Table 10.

The collar chaetae (Fig. 6, P–T), are larger than those of the specimens from the type locality, but otherwise similar. In the abdomen, up to 10 flat trumpet shaped chaetae per fascicle were counted.

The other two Florida samples are similar. However, in sample EJ 67–76, one specimen lacking radioles has 12 thoracic chaetigers on the left and 11 on the right, with the thoracic membranes ending on the 6th and 5th chaetiger, respectively. The samples from Bermuda and Aruba are similar to those from Florida.

LIVE MATERIAL. There are some intra-specific colour variations in *S. ypsilon* sp. nov., as observed in collections from different stations in the Cape Verde Islands:

Stn. 6.D02: Branchial radioles distally orange, proximally pinkish orange, except for a bright red spot where the radioles meet. Thorax is transparently reddish, with two subcutaneous brown spots laterally. Abdomen is pink or orange, with brown sides.

Stn. 7.D03: Distal half of the short radioles banded white and yellowish orange, basal half bright red. Basal radiole parts with oval lens-shaped structures, apparently ocelli. However, after preservation no lenses could be found in this material, not even after staining in methylene blue. Thorax bright red, abdomen orange, with brownish-green granules laterally.

Stn. 7.D05: Radioles transparent, hyaline, with a single row of pigmented spots at the base. No lenses visible, even with a compound microscope. Thorax and abdomen orange-brown. Sides of abdomen show brown granules (in four specimens). In two other specimens the radioles are hyaline, with transverse orange bands and red pigment spots at their bases. The rest of the body is red, otherwise similar to the other four specimens.

ETYMOLOGY. The specific name refers to the Y-shaped internal ridge.

HABITAT AND DISTRIBUTION. As revealed by several scuba dives and littoral surveys in the Cape Verde Islands, *S. ypsilon* sp. nov. occurs on various hard substrata in depths occupied by *S. massiliensis* (Zibrowius) in the Mediterranean. At Stn. 6.D02, for instance, the ceiling of a half metre deep cave, at a diving depth of 14m, was covered with crusts of partially erect tubes of *S. ypsilon*. However, *S. massiliensis*

did not turn up in any of the collections from the Cape Verde Islands. The single, eroded tube of *S. ypsilon* sp. nov. from the dredging station 6.148 (100–200 m) was probably transported down the slope.

Although the Western Atlantic and Cape Verde Islands material show some differences, they appear inadequate to separate them into distinct species. The Western Atlantic range is from Bermuda to Aruba. A species from the Caribbean which has similar internal tube structures, but differs in other respects, is described next.

Spiraserpula paraypsilon sp. nov.

(Figs. 8, A–N; 9, A–R; 3, G)

MATERIAL EXAMINED.

Bonaire (Neth. Ant.): 1. Klein Bonaire, N, half mile E of Westpunt, reef, little sand, corals, 38 m, legit H.A. ten Hove, 1.vii.1970, Stn. 2105A, HOLOTYPE & PARATYPE 2. ZMA V. Pol.3714; PARATYPE 1, BM(NH) 1992.156. 2. Lac, dam, pool in wash of plunging breakers, *Diploria*, *Millepora*, *Porites*, cobble in coarse sand, 50 cm, from corals, legit H. A. ten Hove, 15.vii.1970, Stn. 2122C, (PARATYPES 6–8, ZMA V. Pol.3717). 3. Plaja Frans, on dead coral covered with calcareous algae, little sand, 1.0–1.5 m, legit H. A. ten Hove, 16.vii.1970, Stn. 2110A (portions of tube, 1 incomplete worm, BM(NH) 1992.157). 4. Karpata, steep reef, drop off and flat above, 15–4 m, from living corals, legit H.A. ten Hove, 19.v.1987, Stn. 87–5 (PARATYPES 4–5, USNM 130992).

Curaçao (Neth. Ant.): 5. Cornelisbaai, sandy reef, from the underside of dead plate-shaped coral, 15 m, legit H. A. ten Hove, 15.xi.1988 (PARATYPE 3 USNM 130991) and 17.i.1990 (4 specimens, AM W20338). 6. Piscaderabaai, outer bay in front of Carmabi, rubbish on reef, 10 m, legit H. A. ten Hove, 10–12.i.1990 (19 specimens, ZMA V. Pol.3718, BM(NH) 1992.158–165, FSBC I 39196. 7. Salinja Fuik, reef in front, 20–25 m, legit H. A. ten Hove, 18.i.1990 (25 specimens, NSMT).

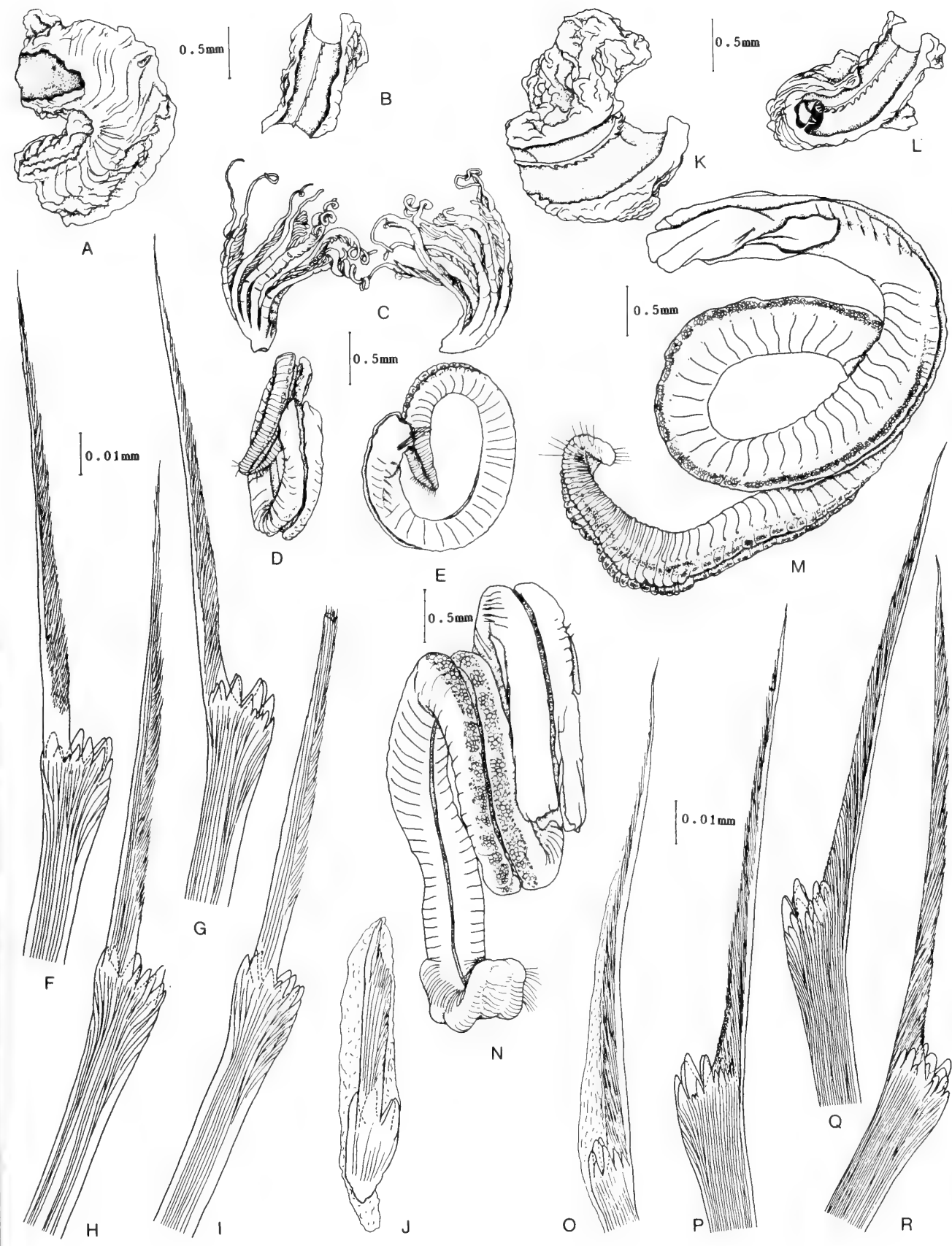
TYPE LOCALITY. Klein Bonaire, Curaçao.

DESCRIPTION.

TUBES: White, flattened, and with a granular overlay. The maximum external diameter of the tube of the holotype is 2.0 mm. A median and about 3 pairs of lateral longitudinal ridges can be observed (Fig. 8, A). In an empty tube from the type locality with a diameter of 1.5 mm, the number of ridges is less distinct (Fig. 8, B). ITS, located within the first formed coiled parts, are translucent white, and very similar to those *S. ypsilon*. They consist of a serrated dorsal ridge along the convex wall (Fig. 8, C) and a Y-shaped ventral ridge along the opposite side (Figs. 8, D; 3, G). The serrations of the dorsal ridge are pointed and directed somewhat posteriorly. Tubes found on asbestos plates (Piscaderabaai) were clearly branching, as described in detail for *S. caribensis* (Fig. 16, A & B).

WORMS: The total length of the holotype is 16.4 mm. With a thoracic width of 0.8mm, it is stouter than *S. ypsilon*. The

Fig. 9 *Spiraserpula paraypsilon* sp. nov. A–N, From Klein Bonaire Stn. 2105A; O–R, from Bonaire, Karpata Stn. 87.5. A–J, From juvenile paratype. A, Tube showing start of external longitudinal ridge and shallow transverse growth markings. B, Posterior tube fragment with serrated dorsal ridge. C, Radioles with long pinnule-free tips, a rudimentary operculum on the left and none on the right. D & E, Two views of body showing pigment patches in both, dorsal and ventral longitudinal abdominal grooves (D), and extent of thoracic membrane (E). F–J, Bayonet chaetae, including one newly formed within the fascicle (J). K–N, From holotype. K & L, Tube fragments (K) and the other from a more posterior coil, with serrated dorsal ridge. M & N, Two views of body showing pigment patches, dorsal and ventral longitudinal abdominal grooves (M), and extent of thoracic membrane (N). O–R, Bayonet chaetae of one specimen.



abdomen is 9.9mm long, with about 98 segments, and capillaries in the last 20.

The pinnule-free tips (Fig.8, E) are quite conspicuous and much longer than those of *S. ypsilon*, being up to about 1.9 mm. They constitute nearly half to more than half the length of the radioles (about 3.7 mm). The number of radioles, 11 on each side, is higher than that of *S. ypsilon* (maximum 8). They bear at intervals what appear to be narrow, transverse, lenticular lacunae. Two pigmented prostomial ocellar clusters are present.

The rest of the body (Fig.8, F) is similar to that of *S. ypsilon* in many respects. In alcohol, the abdomen has an overall pinkish colour, with clusters of reddish-brown pigmented cells ventro-laterally.

Thoracic chaetigers number 7 on both sides. Thoracic membranes end on the third thoracic chaetiger (second uncinigerous segment) on both sides of the thorax. Paired ventral thoracic glands were not seen.

A collar fascicle of the holotype has five fully formed bayonet chaetae, and a developing one deep within. A paratype from Karpata has 6 fully formed bayonets and one newly forming one within the fascicle. Each bayonet chaeta consists of a long, narrow serrated blade, and a considerably expanded basal boss bearing several moderately large, somewhat pointed teeth (Fig.8, G-L). The serrations are short and fine proximally, but longer and pilose distally. The unserrated notch may be very short, up to about twice the length of the longest teeth, or almost lacking (Fig.8, I). The thoracic and anterior abdominal uncini bear 5 teeth in a single row. They differ from all the other known species of the subgenus in possessing minute denticles on their sides (Fig.8, M,N).

The adaptations of the worm in relation to ITS are similar to those of *S. ypsilon*. The dorsal longitudinal abdominal groove is applied to the serrated dorsal ridge of the tube, and the Y-shaped ventral ridge is enclosed within a ventral abdominal groove. Within the latter, a cord-shaped abdominal ridge fits into the gutter-shaped part of the Y.

The paratype from the type locality is a juvenile. Its tube (Fig.9, A) shows faint transverse grooves mainly, but the beginnings of a granular overlay and longitudinal ridges can also be seen. ITS and adaptations of the body are identical to those of the holotype (Fig.9, B,K,L). Measurements and counts of the worm are as follows: Length 6.2 mm, thoracic width 0.5 mm, radiolar length 2.1 mm, pinnules 1.1 mm, abdomen 4.2 mm, 53 segments, with capillaries on the last 10. The number of thoracic chaetigers, ending of the thoracic membranes (Fig.9,E), and colour, are the same as in the holotype.

The 7 pairs of radioles already approach the maximum number in other material, except the holotype, and their long pinnule-free tips are similar to those of the holotype (Fig.9, C). However, there is a very short and slender rudimentary operculum on one side, while it is lacking on the other (Fig.9, C), indicating that both may become completely lost in older specimens (holotype). A similar condition is found in one of the specimens from Karpata (below).

Collar fascicle with four fully formed bayonet chaetae (Fig.9, F-I) and a developing one deep within (Fig.9, J). Their basal bosses are not as expanded as in the holotype and the blades are shorter. The uncini are similar to those of the holotype.

The tubes of the three specimens from Karpata agree with those from the type locality in being white externally, pinkish internally, and bearing the Y-shaped ventral ridge and ser-

rated dorsal ridge. The serrations of the latter bear posteriorly directed tapered tips (Fig.9, K,L). The radioles of all specimens are detached, highly contracted, and do not clearly show the extent of the pinnule-free tips. One crown has a short rudimentary operculum on each side, the second has a rudimentary operculum on one side but lacks it on the other, and the third half crown has a rudimentary operculum which is very reduced and filamentous. The thoracic width ranges between 0.5 mm and 0.7 mm. The abdomen of the longest specimen is 10.8 mm long and has about 59 segments, with capillaries on the last six; that of the shortest is 7.3 mm, but has about 86 segments, with capillaries on the last six. The numbers of radioles, thoracic chaetal tufts and the extent of the thoracic membranes in the three specimens is provided in Table 11.

In two specimens the broad thoracic membranes are folded outwards against the sides of the thorax (Fig.9, M,N). Bayonet collar chaetae (Fig.9, O-R) are similar to those of the holotype, but lack an unserrated notch. Thoracic and anterior abdominal uncini are also similar to those of the holotype, with 4 or 5 teeth in a single row. Flat trumpet chaetae number 6-8 in a bundle. Preserved in alcohol, the abdominal segments show clumps of reddish-brown pigmented cells ventrolaterally, and of larger yellowish or orangeish cells ventrally (Fig.9, N).

The tube of the single juvenile paratype from Curaçao resembles that of the holotype; its diameter is 1.5 mm. The worm has 6 radioles on the left and 5 on the right. As in the specimens from Bonaire, the pinnule-free tips are very long. However, both rudimentary opercula have already been lost at this stage. The thorax is 0.5 mm wide and has 7 pairs of chaetigers. The thoracic membranes end on the third thoracic chaetiger. Two clusters of prostomial ocelli are present. Thoracic glands were not seen. The chaetae also agree with those of the specimens from Bonaire. In recently collected material (Curaçao, Piscaderabaai, 10.i.1990), thoracic membranes end at 4/5, 4/4 respectively; the pinnule-free tips generally are very long, rarely short; rudimentary opercula are present in four specimens, absent in three.

LIVE MATERIAL. According to the field notes, rudimentary opercula could not always be found, even in living specimens from Curaçao with radioles extended. The colouration of the radioles is somewhat variable, often (transparently) whitish to creamish, rarely yellowish to slightly orange or even completely hyaline. At the base of the radioles there is a series of up to six pairs of reddish spots, absent however in the dorsal- and ventralmost radioles. Body predominantly orange-brownish with up to 15 greenish-brown granules per segment ventro-laterally in the abdomen and dorsally in the thorax.

ETYMOLOGY. The specific name *paraypsilon* indicates the close resemblance of the species to *S. ypsilon*.

HABITAT AND DISTRIBUTION. Occurs in shallow, clear, oce-

Table 11 *S. paraypsilon* sp. nov. Meristic and other data from specimens.

Specimen nos.	1	2	3
No. of radioles	8/?	8/8	8/7
No. of thoracic chaetal tufts	?/?	8/9	7/7
Thoracic membrane ends	?/?	3/3	3/3

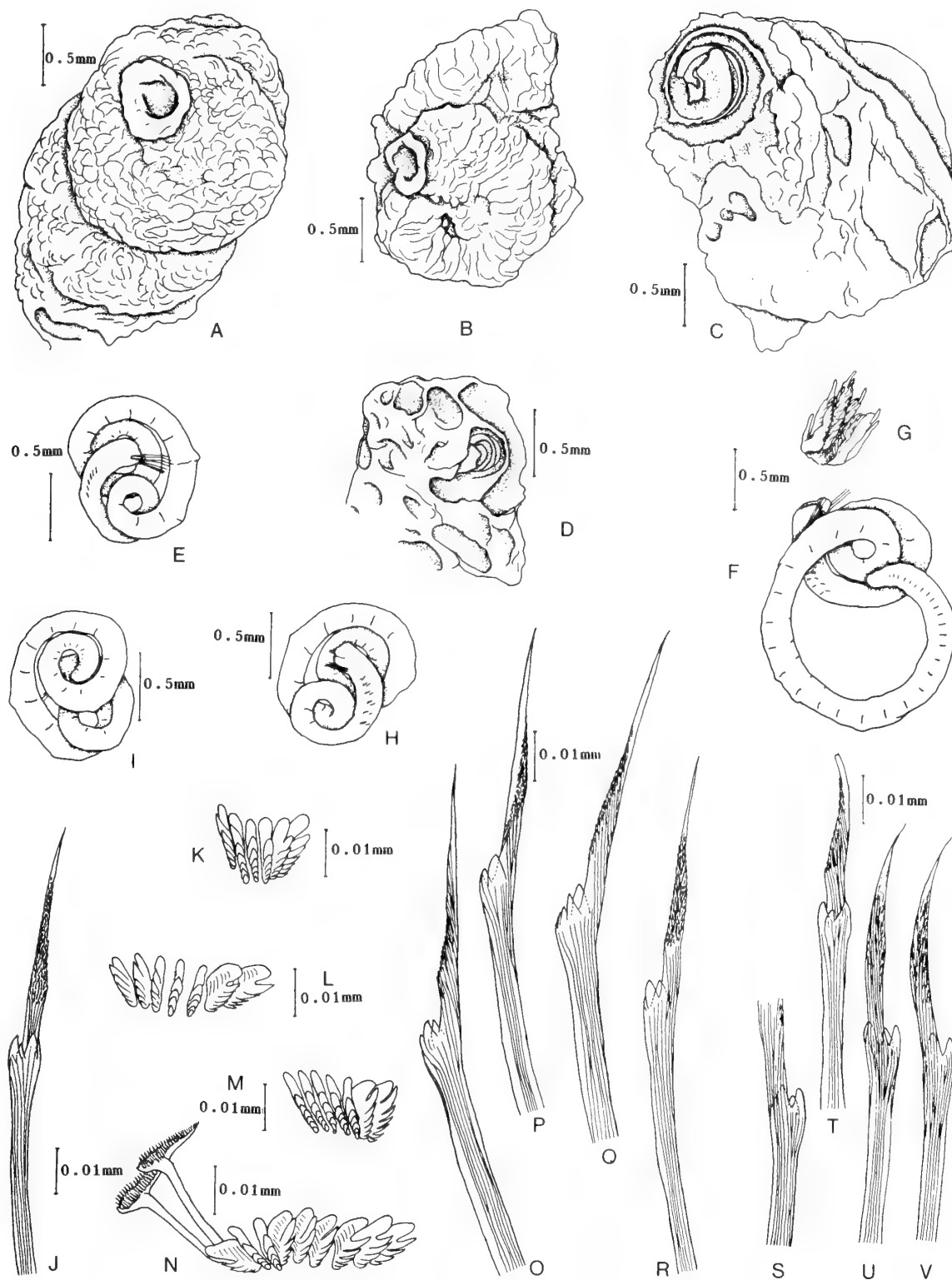


Fig. 10 *Spiraserpula singularis* sp. nov. From type series. A & B, Two tubes, the second one younger. C, Substratal view of first formed coil showing V-shaped dorsal ridge; a ventral ridge is absent. D, Same, smaller specimen. E, Paratype. F & G, Holotype and radioles. H-L, From whole mount of another paratype: H & I, Two views of worm; J, only available bayonet chaeta; K, L, thoracic uncini; M, anterior abdominal uncini. M-R, From whole mount of another specimen: N, anterior abdominal uncini and flat trumpet chaetae; O-R, Bayonet collar chaetae, two present per side. S-V, Bayonet chaetae from whole mount of third specimen.

anic waters, at depths of up to 40 m on coral reefs. Hitherto collected only from Bonaire, and Curaçao, in the Caribbean.

Spiraserpula singularis sp. nov.

(Figs.10, A–V; 3, B; Pl.2, E & F)

MATERIAL EXAMINED.

Puerto Rico : 1. Isla Matei, near buoy of Marine Institute, vertical reef with surge channels, no sand, from living corals, 29–33 m, legit H. A. ten Hove, 2.x.1970, Stn. 2136A, (HOLOTYPE & 3 PARATYPES, ZMAV.Pol.3710).

Curaçao, (Neth. Ant.): 2. Salinja Fuik, reef in front, marine park, 20–25 m, legit H. A. ten Hove, 18.i.1990 (2 specimens BM(NH) 1992.166–167). 3. Piscaderabaai, outer bay, W of entrance, sandy reef, 20 m, from underside of coral debris, not in sediment, legit H. A. ten Hove, 12.i.1990 (3 specimens, BM(NH) 1992.168–170).

TYPE LOCALITY. Puerto Rico.

DESCRIPTION.

TUBES: White, very tiny, one of the smallest species in the genus. They may occur in mutually bonded aggregations of a few individuals, or singly. Their coil diameters range from 1.2–1.3 mm. A granular overlay is present (Fig.10, A,B), which makes the external diameters of the tubes (0.5–0.6 mm) considerably larger than their internal diameters (0.2–0.25 mm). Their apertures bear small, somewhat lobed, peristome-shaped extensions (Fig.10, A,B), similar to those found in *S. massiliensis*.

ITS consist of a V-shaped dorsal ridge, actually an inverted V, along the convex side of the first formed coil (Figs.10, C,D; 3, B). The two arms of the V are broader and outwardly curved posteriorly, and their edges are smooth. Anteriorly the dorsal ridge is a smooth plate only. A ventral ridge is absent. When the worm is withdrawn into the tube, the posterior, mid-dorsal part of the abdomen is applied to the dorsal ridge.

WORMS: Four specimens were taken out of their tubes (Fig.10, E–I). The holotype (Fig.10, F), which is the largest, is only 5.7 mm long, 0.2 mm wide in the thorax, and its abdomen is 4.6 mm long. There are four pairs of radioles which, including the short and slender pinnule-free tips (Fig.10, G), are about 0.55 mm long. There is a rudimentary operculum on each side. Radioles are missing in the other three specimens. However, a detached operculum was found in the vial containing the specimens, and it is not certain whether it belongs to one of them or another species.

Two clusters of prostomial ocelli are present. Five or six globular ventral thoracic glands are present, more or less arranged in a V. The numbers of thoracic chaetigers on the two sides in the four specimens are: 9/9, 9/8, 8/8, and 7/7. It was not possible to establish the extent of the thoracic membranes due to the extremely small size of the worms. An apron is, however, absent. One paratype with an abdominal length of 1.95 mm has 29 segments, with capillaries on the last 5, and another 3.0 mm long with 39 segments, but the capillaries cannot be seen, having probably been damaged.

There are two bayonet chaetae in each collar fascicle. They have moderately long serrated blades and 2–4 teeth on the basal boss and some accessory ones (Fig.10, J, O–V; Pl.2, E). The unserrated notch is 1/5 the length of the blade. Thoracic uncini (Fig.10, K,L) and anterior abdominal uncini (Fig.10, M,N) have 6 and 4–6 teeth, respectively, all in a single row. The middle abdominal uncini are rasp-shaped (Pl.2, F), with

up to 3 transverse rows of teeth above the single anterior tooth. The abdominal segments bear 1 or 2 flat trumpet chaetae in each bundle; one side is thickened into a claw-shaped process (Fig.10, N).

REMARKS. In the comparison with other Caribbean species, *S. singularis* would key out mainly on the absence of a ventral longitudinal ridge/row of teeth and probably also the absence of an operculum. So far, the presence of an operculum has been observed only in a doubtful field identification. The form of thoracic glands, shape of dorsal ridge and collar chaetae are similar to those in *S. plaiae*.

ETYMOLOGY. *singularis* (Latin)= unique; referring to the unique ITS.

HABITAT AND DISTRIBUTION. *S. singularis* sp. nov. appears to be a shallow water coral reef dweller. It has hitherto been collected only from Puerto Rico and Curaçao.

Spiraserpula karpatisensis sp. nov.

(Figs.11, A–K; 3, N)

MATERIAL EXAMINED.

Bonaire (Neth. Ant.): 1. Karpata, reef, 10 m, cryptic, legit H. A. ten Hove, 9.xi.1988 (HOLOTYPE, ZMA V.Pol.3712; PARATYPE, BM(NH) 1992.171).

Curaçao (Neth. Ant.): 2. Reef in front of Salinja Fuik, buoy 13 of Marine Part, 20–30 m, corals and sandy/silty areas in equal amounts. From under side of coral debris, not in sediment, legit H. A. ten Hove, 18.i.1990 (1 specimen, ZMA V. Pol. 3875).

TYPE LOCALITY. Bonaire (Netherlands Antilles).

DESCRIPTION.

TUBES: Pink, quite small, and lack longitudinal ridges. A pink translucent granular overlay is present (Fig.11, A). The tubes of both the types are coiled upon themselves, one much more than the others (Fig.11, D). One has an erect part 2.0 mm long, and a funnel-shaped, outwardly curved peristome (Fig.11, A), while the other has a somewhat thickened anterior end (Fig.11, D,E). The pink colouration gradually fades to white towards the anterior end. The diameter of the tubes is 0.6–0.7 mm in the attached parts, 0.4–0.6 mm in the erect parts.

ITS consist of a serrated ventral ridge and an unserrated dorsal ridge, with a sharp edge in cross-section (Fig.3, N). The dorsal ridge may be absent (Fig.11, B,C), or greatly reduced (Fig.11, D). In the latter it can be seen as a short crescentic ridge through the broken end of one of the coils. The serrated ventral ridge is regularly present (Fig.11, B, C, and bottom left of D).

WORMS: The holotype is incomplete posteriorly (Fig.11, F), broken in three parts, with a total length of 4.3 mm. An operculum and 4 radioles are present on the left side; the radioles on the right are missing. The length of the radioles is approximately 0.8 mm, with a pinnule-free tip of 0.1 mm. The operculum (Fig.11, G,H), is 0.26 mm long, and 0.28 mm in diameter; inclusive of peduncle it is about 1 mm long. Although bell-shaped, it is slightly zygomorphic, and has numerous fine lobes, similar to that of *S. plaiae* described in this paper. Branchial eyes have not been observed in the fresh material. Two clusters of prostomial ocelli are present. The thorax has 8 chaetigers on each side. The thoracic membranes extend to the third chaetiger on the left (Fig.11,

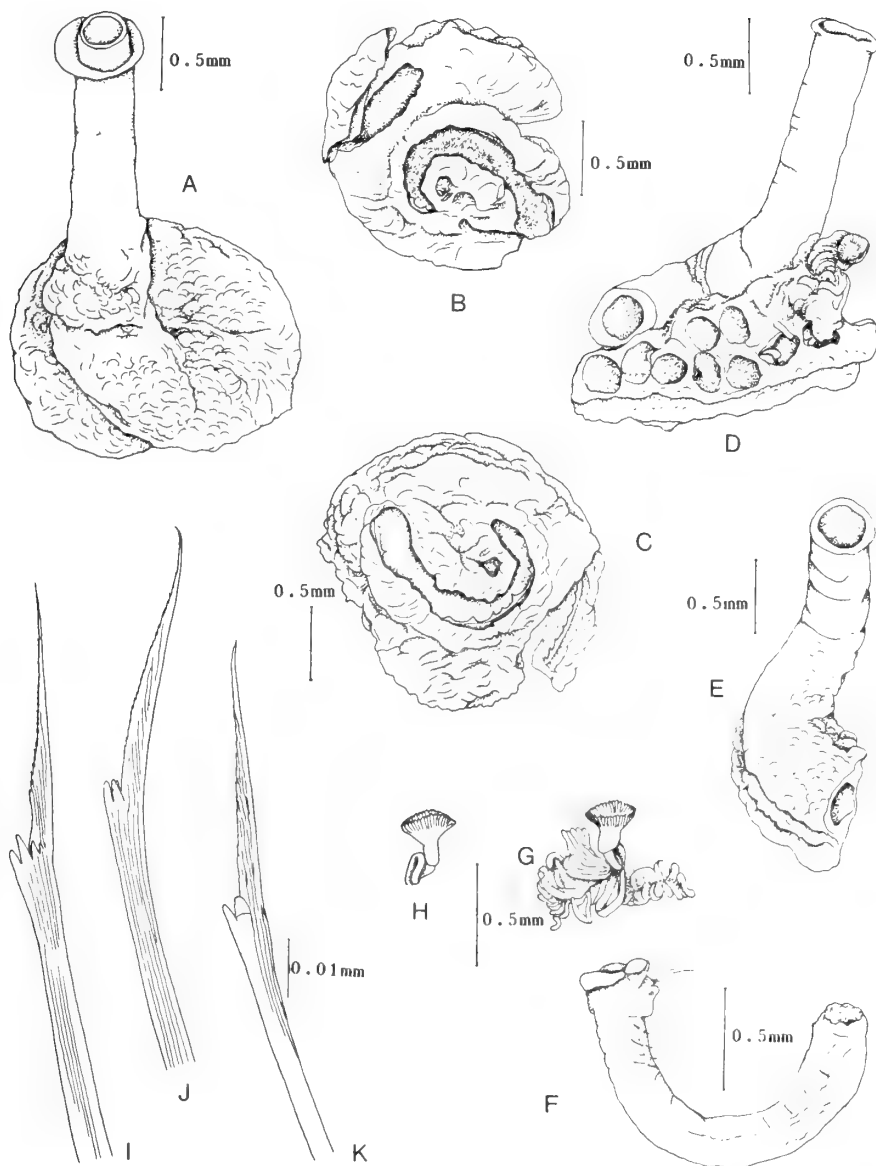


Fig. 11 *Serpula karpatensis* sp. nov. A, Tube with granular overlay, erect part and funnel-shaped peristome. B & C, Substratal view of two tubes, opened to show internal serrated ventral ridge along convex wall, but absence of dorsal ridge. D, Aggregation of tubes, some sections showing a very short crescentic dorsal ridge. E, Erect part from same aggregation showing somewhat thickened distal end; granular overlay. F, Anterior end of holotype showing collar and thoracic membrane. G & H, Two views of zygomorph operculum. I-K, Bayonet chaetae.

F) and the fourth on the right. It is not certain whether ventral thoracic glands are present, but see note on live material below.

Each collar fascicle bears 3 bayonet chaetae (Fig. 11, I-K), with moderately long, finely serrated blades, a moderately long unserrated notch, and 3 teeth on the basal boss; the third tooth may sometimes be difficult to observe and may be reduced to a scar. Thoracic uncini have 6 (exceptionally 7) teeth, anterior abdominal uncini 5, arranged in a single row. The middle abdominal uncini are rasp-shaped, with 3-5 teeth above the single anterior tooth. At least 35 abdominal chaetigers are present, the last 7 with capillary chaetae. Abdominal flat trumpet chaetae number 2-3 per bundle.

The specimen from Curaçao agrees in most details with the

type material. Its numbers of radioles are 5/5, a long filamentous rudimentary operculum is present opposite the operculum, and it has 38 abdominal chaetigers.

LIVE MATERIAL. As observed in material collected in 1990, radioles are transparently lemon. Thorax ventrally with 5 bright red globules arranged in a V, presumably thoracic glands.

ETYMOLOGY. named after the type locality, the coral reef in front of the Sentro Ekologiko, Karpata.

HABITAT AND DISTRIBUTION. A shallow water cryptic reef dweller. Has hitherto been recorded only from its type locality in Bonaire, and Curaçao.

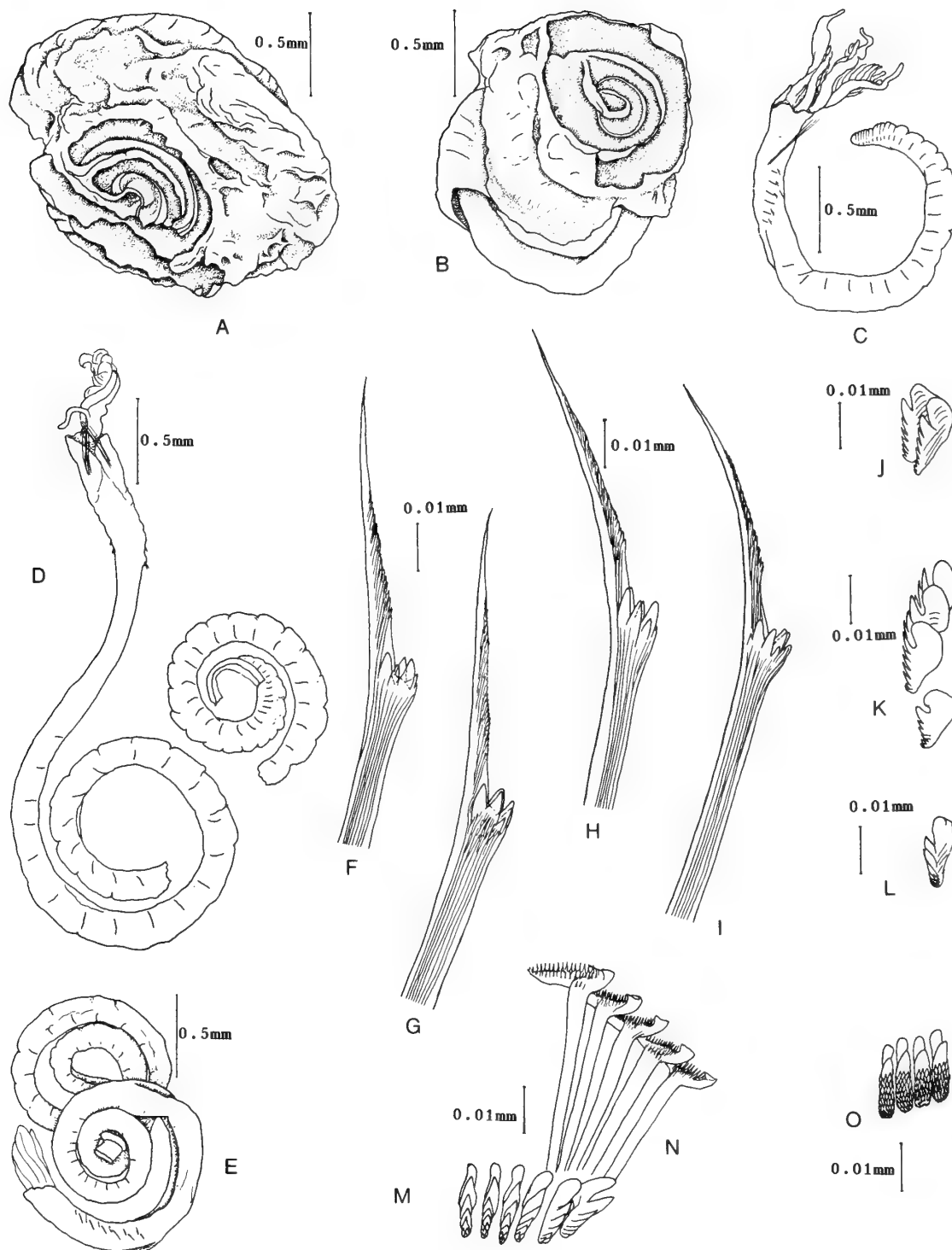


Fig. 12 *Spiraserpula zibrowii* sp. nov. From type specimens. A & B, Substratal view of two tubes opened to show the unserrated dorsal ridge. The serrated ventral ridge consists here of a row of isolated teeth, but is a continuous ridge in the remaining material. C, Juvenile paratype. D, Older specimen (holotype) broken in two. Anterior part with right rudimentary operculum; posterior abdomen with part of dorsal ridge attached to mid-dorsal groove. E, Paratype. F & G, Two bayonet chaetae from holotype; H & I, two bayonet chaetae from paratype. J–O from paratype. J, Thoracic uncini of small specimen with single row of teeth anteriorly and a cluster of more than one row posteriorly. K, Similar uncini from first abdominal torus. L, Uncini from second abdominal torus; there are less teeth in a single row. M & N, Anterior abdominal uncini, and flat trumpet chaetae with large lateral tooth. O, Posterior abdominal uncini; except for a single anterior tooth, the uncini are rasp-shaped, with teeth in several rows.

Spiraserpula zibrowii sp. nov.
(Figs.12, A–N; 3, O; Pl.4, A–D)

MATERIAL EXAMINED.

Curaçao (Neth. Ant.): 1. Lagoon of San Juan, E, raised reef, lagoon side, *Halimeda* present, limestone cobbles, 10–15 cm; from up to 20 cm deep crevices between cobbles, legit H. A. ten Hove, 29.vi.1970, Stn. 2043 [HOLOTYPE & PARATYPES 3–5: ZMA V.Pol.3707; PARATYPES 1 (slide), 2 (worm & tube fragments), and 7 (empty tube: BM(NH) 1992.148–150); PARATYPE 6: USNM 130980 (unopened tube)].

Bonaire (Neth. Ant.): 2. Kralendijk, Flamingo Beach Hotel, from corals, partly in sand, 45 m, legit H. A. ten Hove, 27.vii.1970, Stn. 2115D, (4 empty tubes, BM(NH) 1992.151–155). 3. 250 m N of Witte Pan, sandflat below reef, 47 m, mainly from the side of boulders, partly buried in sand, legit H. A. ten Hove, 3.vii.1970, Stn. 2117B (4 empty tubes, ZMAV. Pol. 3708).

TYPE LOCALITY. Curaçao (Netherlands Antilles).

DESCRIPTION.

TUBES: Whitish, very tiny, and coiled upon themselves like spirorbids, either individually (Fig.12, B), or in mutually bonded aggregations of a few individuals. The direction of coiling may reverse (see below). A fine granular overlay is present. Longitudinal ridges are absent, but fine, smooth, transverse growth markings are present. Juvenile tubes are white. Although older tubes are white posteriorly, they have a greyish-brown overlay anteriorly. The diameter of an individual coil is 0.73 mm, with a tube diameter of 0.18 mm. The maximum tube diameter is only 0.44 mm, which is the smallest among the known species of the genus.

ITS consist of a serrated ventral ridge and an unserrated dorsal ridge (Fig.12, A,B). The ventral ridge may consist either of a continuous row of serrations, or only of a short row of small separate teeth (Figs.12, A,B; 3, O). The dorsal ridge is colourless and transparent, wedge- to Y-shaped in cross-section, with its edges curved in places; it is spiral on a columella-shaped axis when the tube is coiled upon itself. Lateral ridges have not been found. The interior of the tube may have a creamish lining.

One tube is coiled in one direction proximally, and in the opposite direction distally. In the proximal coil the ITS are similar to those described above. However, the distal coil has only a columella-shaped axis with a dorsal ridge, which became detached from the tube and is shown *in situ* (Fig.12, E); a serrated ventral ridge is absent here.

The mid-dorsal and mid-ventral longitudinal grooves of the abdomen are applied to the unserrated dorsal ridge (Fig.12, D) and serrated ventral ridge of the tube, respectively.

WORMS: Measurements and meristic data are presented in Table 12.

The right branchial half of the holotype (left missing) shows a rudimentary operculum. The latter is present on both sides in the first paratype, but not in the second which is a juvenile. The numbers of radioles on both sides are 7/3, 4/4 and 3/4, respectively. The pinnule-free tips are about 1/5–1/7 of their total length.

Two clusters of prostomial ocelli are present. The numbers of thoracic chaetal tufts on both sides in the three specimens are: 7/7, 8/7 and 8/7, respectively. The thoracic membranes end on chaetigers 3/3 in the holotype and 4/4 in the juvenile paratype; they are damaged in the second paratype. Two

Table 12 *S. zibrowii* sp. nov. Measurements and meristic data from Holotype and two paratypes.

	Total length (mm)	Thoracic width (mm)	Abdomen		
			Length (mm)	Number of segments	capillaries on
Holotype	9.7	0.23	8.5	54	4
Paratype 1	7.0	0.18	5.8	43	7
Paratype 2	3.4	0.18	2.1	27	9

translucent ventral thoracic glands are present, although not as easily discerned as in some of the other species.

There are 2 or 3 fully developed bayonet chaetae per side in the juvenile, 4 in the older specimens. They have moderately long serrated blades, an unserrated notch which is about 1/4–1/5 the length of the blade, and 4 or 5 somewhat large teeth and some accessory ones on the basal boss (Fig.12, F,I; Pl.4, A). The thoracic uncini have a single row of 6–7 teeth (Pl.4, B). Anterior abdominal uncini bear a cluster of small teeth in two to seven rows at their posterior ends, and a single row of larger teeth anteriorly; this type of uncini may occur in juvenile specimens also (Fig.12, J–M). The posterior abdominal uncini are, however, similar to those of the other species in being rasp-shaped, with 6 transverse rows of 2–5 teeth each, except for the single anterior tooth (Fig.12, O; Pl.4, C). The abdominal flat trumpet chaetae number about 5 per bundle. Their somewhat triangular, curved distal ends are thickened and hooked at one end, and drawn out into an acute angle at the other (Fig.12, N; Pl.4, D). Up to 54 abdominal segments are present, the last 4–9 with capillary chaetae.

REMARKS. The collections from Bonaire, a mere 50 km from Curaçao, consist of a total of 8 empty tubes whose ITS are identical with those of the present species. The largest tube from Witte Pan has a coil diameter of 2.2 mm; two tubes have erect portions with peristomes. Three tubes are white. The fourth is creamish in colour, with a creamish interior lining. Fine transverse growth markings are present on all. The serrations of the ventral ridge are arranged on a low longitudinal ridge in some of them.

In the absence of worms, and the markedly different habitat from which they were collected (at a depth of 45–47 m), these tubes cannot be conclusively identified as *S. zibrowii*.

ETYMOLOGY. named after H. Zibrowius, who recognized some of these small species as being new.

HABITAT AND DISTRIBUTION. Appears to be a shallow water species inhabiting crevices between boulders and their undersides in sandy areas close to coral reefs. Hitherto collected from Curaçao. Two uncertain records from Bonaire.

Spiraserpula plaiae sp. nov.
(Figs. 13, A–T; 3, K)

MATERIAL EXAMINED.

Curaçao (Neth. Ant.): 1. Salinja Fuik, near Ceru Preekstul, open reef, coral debris, 33 m, from limestone boulder on sand, legit H. A. ten Hove, 18.ix.1970, Stn. 2088A (HOLOTYPE & PARATYPES 1 & 5: ZMA V. Pol.3713;

PARATYPES 2, 4, & 6: BM(NH) 1992.173–174; PARATYPE 3: USNM 130990). 2. Reef in front of Salinja Fuik, buoy 13 of marine park, coral debris, 18–27 m, legit H. A. ten Hove, 18.i.1990 (4 specimens, ZMA V. Pol.3874). 3. Cornelisbaai, E, steep reef, coral debris, 18–26 m, legit H. A. ten Hove, 17.i.1990 (6 specimens, ZMA V. Pol.3873). 4. Piscaderabaai, outer bay W of entrance, sandy reef, coral debris, legit H. A. ten Hove, 12.i.1990 (5 specimens, ZMA V. Pol.3872).

TYPE LOCALITY. Curaçao (Netherlands Antilles).

DESCRIPTION.

TUBES: White to greyish-brown, occurring either individually coiled upon themselves (Fig.13, A), or in mutually bonded aggregations of a few individuals (Fig.13, B). They are sub-circular in cross-section, with faint lateral ridges, and bear fine smooth transverse ridges, and often have erect anterior ends (Fig.13, A,B). A fine opaque granular overlay is present (Fig.13, B), which can be seen under special illumination only. Their external diameter attains 1.0 mm, their erect portions somewhat smaller. The inside of one tube has a light caramel coloured lining.

ITS consist of a serrated ventral ridge along the concave side of the tube (Fig.13, C–E, H), which may not be well developed and represented only by a few isolated or coalesced teeth slanting backwards (Fig.13, F), and a smooth dorsal ridge on the convex side (Figs.13, F,G; 3,K). The latter is wedge-, T to Y-shaped in cross-section. In specimens coiled upon themselves, the dorsal ridge occurs spirally on a columella-shaped axis (Fig.13, I). A short accessory latero-dorsal ridge, which tapers anteriorly and posteriorly, may also be present on either side (Fig.13, F). Their edges are unthickened.

In life, the mid-ventral and mid-dorsal longitudinal grooves of the abdomen are applied to the serrated ventral and smooth dorsal ridges, respectively, of the tube (Fig.13, G).

WORMS: Six specimens were taken out of their tubes. The abdomen is complete in only one. Even though preserved in alcohol, the abdominal segments still show clusters of pigmented specks laterally, light yellowish in one specimen, light to bright orange in two, light to dark brown in two, and uniformly caramel coloured in another.

Five specimens have an operculum on one side and a rudimentary operculum on the other; the branchial crown is partly missing in the sixth. The length of the operculum and peduncle varies from 1.0 mm in a juvenile paratype to 1.8 mm in the holotype. The operculum itself is 0.4–0.5 mm long, 0.3–0.5 mm wide. It is zygomorph, attached to the peduncle eccentrically, and bears numerous (up to 50) radii (Fig.13, K–M). The distal diameter of the peduncle is 1/3 to 2/3 that of the opercular base. The numbers of radioles on both sides are 6/5, 5/4, 4/5, 4/4 and 4/3. They end in short slender pinnule-free tips, which are about 1/5 to 1/7 the length of the radioles (Fig.13, K). The only complete specimen (Fig.13, J), is 4.9 mm long, with 42 abdominal segments, the last 10 with capillaries. However, in another specimen, which

is incomplete (Fig.13, M), 76 abdominal segments could be counted.

Two clusters of prostomial ocelli are present. The numbers of thoracic chaetal tufts are 11/7, 9/9, 9/8, 8/8, 6/6. Thoracic membranes extend to chaetigers 6/5, 4/4, 4/3, 4/?, and they are damaged on both sides in the fifth. Two groups of transparent to translucent ventral thoracic glands, arranged in a V, and of unknown function, are present. Further studies are needed to find out if they could be responsible for secreting the caramel coloured inner lining of the tube.

Collar fascicles bear 2 or 3 fully formed bayonet chaetae each, and a newly formed one deep within the bundle. Each bayonet chaeta consists of a moderately long blade, a moderately long unserrated notch which is 1/3 to 1/4 the length of the blade, and 2–4, seldom 5, teeth on the basal boss (Fig.13, N–T). The teeth are comparatively larger as their number decreases (Fig.13, Q–T), and they may be accompanied by one or two accessory teeth (Fig.13, O,P,S). Thoracic uncini possess 5–7 teeth in a single row (Fig.13, U). Abdominal uncini are similar, with 5–6 teeth; anteriorly saw- and rasp-shaped uncini may occur in a single row, posteriorly all uncini are rasp-shaped.

LIVE MATERIAL. As observed in material collected in 1990, radioles are faintly yellow to lemon, operculum is transparent, almost colourless. Thorax ventrally with 2–4 bright red to orange globules arranged in a V, presumably thoracic glands; body transparent with yellow tinge, brownish gut.

ETYMOLOGY. Named after Gayle Plaia who, when working at the Florida Marine Research Institute, first observed ITS in one of the species, *S. ypsilon*, from the Gulf of Mexico.

HABITAT AND DISTRIBUTION. *S. plaiae* is a shallow water species occurring in coral reefs, and has hitherto been collected only from the type locality.

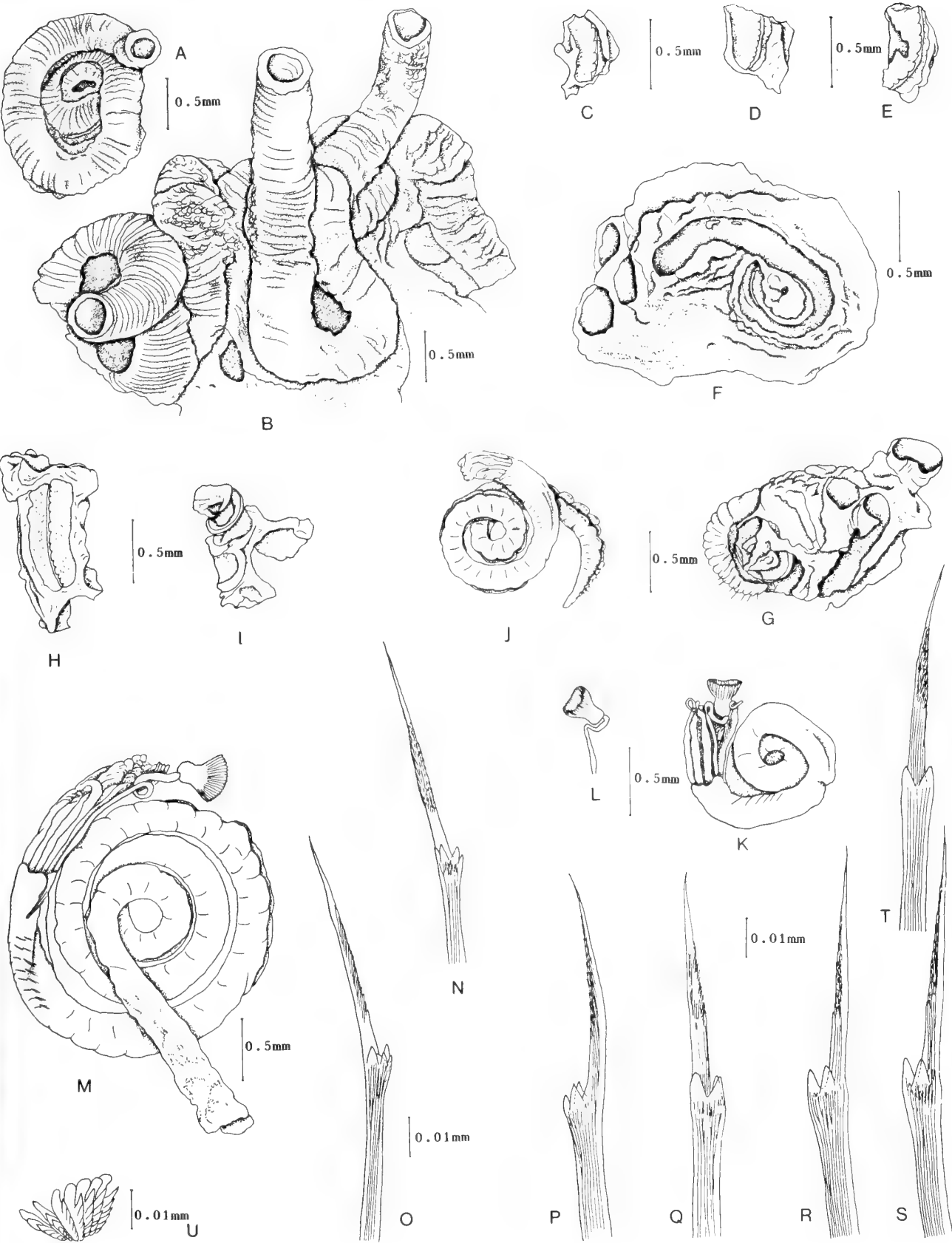
Spiraserpula caribensis sp. nov.

(Figs. 14, A–M; 15, A–Y; 16, A–K; 3, L; Pl.4, E & F; Pl.5, A–E)

MATERIAL EXAMINED.

Curaçao (Neth. Ant.): 1. Awa Blancu, coral debris barrier, 20–30 cm, legit H.A. ten Hove, 15.ix.1975, Stn. 75–38 (HOLOTYPE & 3 PARATYPES: ZMA V.Pol.3715; 2 PARATYPES USNM 130987; 4 PARATYPES each: AM W20157, NSMT, ZMK). 2. Awa Blancu, 3–4m, legit H. A. ten Hove, 14.x.1975, Stn.75–37 (1 specimen, HUJ). 3. Awa Blancu, coral debris, near Lagoen Blancu, 30–50 cm, legit H. A. ten Hove, 30.vii.1970, Stn. 2090 (several subsamples BM(NH) 1992.25–31, FSBC I 39195, ZMA V. Pol. 3716, ZMB). 4. Lagoen Blancu, coral debris barrier, *Halimeda*, 20–30 cm, legit H. A. ten Hove, 15.ix.1975, Stn.75–36 (2 out of several specimens, RMNH 18174). 5. Awa di Oostpunt, coral debris barrier, 30–50 cm, legit H. A. ten Hove, 3.x.1975, Stn.75–77 (1 out of few specimens, BM(NH) 1992.10–11. 6. St. Jorisbaai, Peninsula Groot St.

Fig. 13 *Spiraserpula plaiae* sp. nov. A, Aggregation of tubes, showing fine transverse growth markings, granular overlay in places. B, Juvenile tube. C–E, Fragments of tubes showing serrated ventral ridge (C & D, paratype 3), (E, paratype 2). F, Holotype showing variant form of ventral ridge with isolated teeth, and ventro-lateral ridge. G–I, Paratype 4: G, posterior end of tube and worm. H, Portion of tube showing ventral ridge. I, Dorsal ridge on columella-shaped axis. J–L, Two views of paratype 4, and its operculum: J, (Operculum not seen), ventral longitudinal abdominal groove, and dorsal groove within 2nd coil; K, showing operculum; L, Another view of operculum. M, Paratype 2. N & O, Bayonet chaetae from holotype. P–T, Bayonet chaetae from paratype. U, Thoracic uncini from holotype.



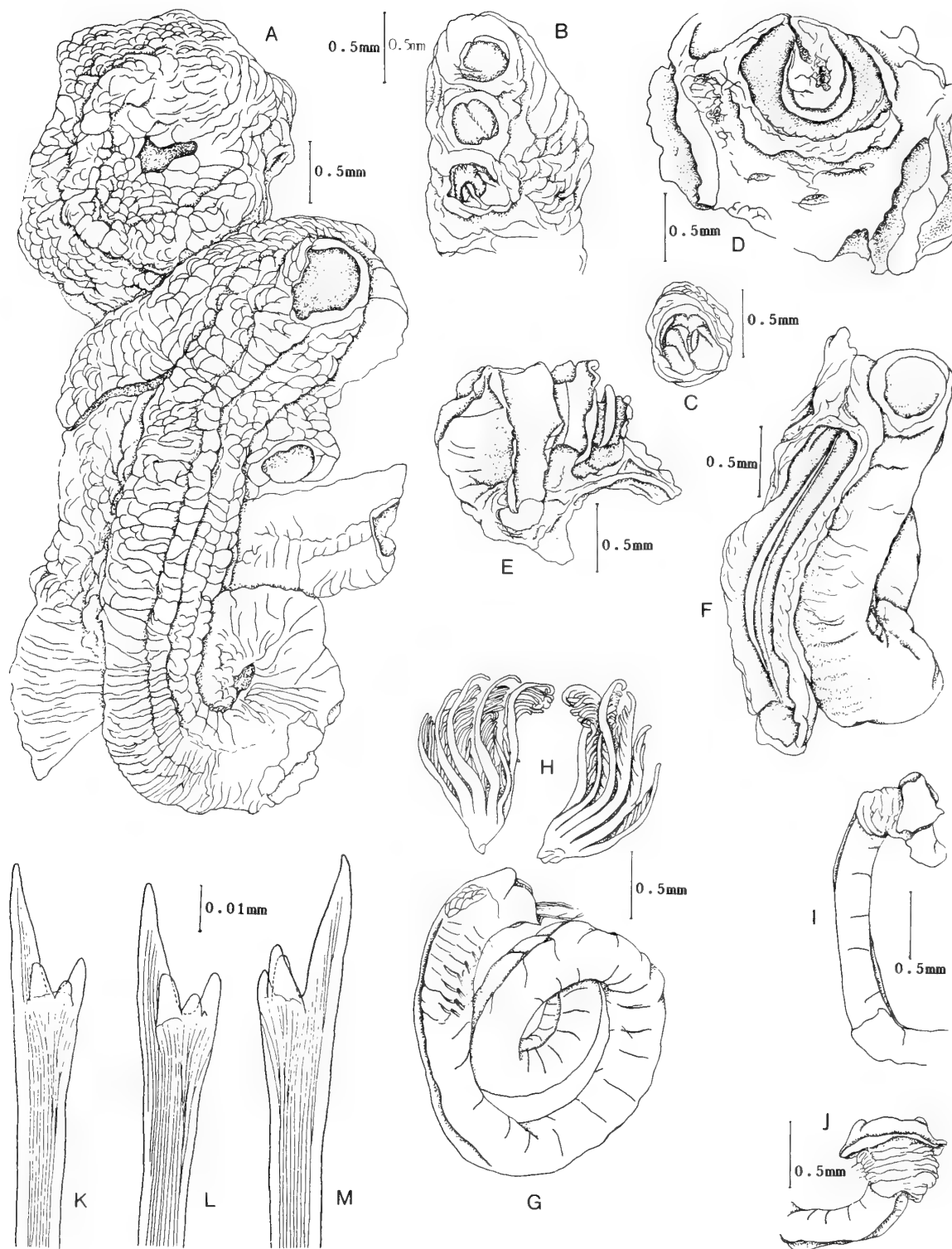


Fig. 14 *Spiraserpula caribensis* sp. nov. A-J, From Florida, Stock Island, Stn. 7B. A, Tube with granular overlay and longitudinal ridges. B-F, ITS seen in various tube fragments: B, bottom cross-section showing median dorsal ridge on convex wall, narrow lateral ridge on either side, and serrated ventral ridge (barely visible); middle cross-section with serrated ventral ridge along concave wall; C, ventral ridge in sectional view (barely visible), and dorsal and lateral ridges; D, substratal view of first formed coil of tube opened to show smooth dorsal and serrated ventral ridge; E, smooth dorsal ridge in the first formed coil, on the right; F, uncoiled part of tube showing smooth dorsal ridge tapering at both ends. G, Anterior end of specimen, with thoracic glands, and showing dorsal and ventral abdominal grooves. H, Radioles of same specimen with left and right filamentous rudimentary opercula. I & J, anterior end of a worm with two views of collar. K-M, Bayonet chaetae.

Joris, muddy pebbles, *Thalassia* flat, few corals, from limestone boulders, 30 cm, legit H. A. ten Hove, 10.ix.1970, Stn.2096 (2 out of several specimens, BM(NH) 1992.20-24, RMNH 18175). 7. St. Jorisbaai, Koraal Tabak, Punta Blanco, undersides of boulders, on rocky debris, 20-30 cm, legit H. A. ten Hove, 15.xi.1988, 9.i.1990, near Stn.75-30 (5 out of several specimens, MCZ, ZMH). 8. St. Jorisbaai, entrance channel, W, boulders and large metal poles in surf; from undersides crusts of *Spiraserpula*, legit H.A. ten Hove, 16.i.1990 (clusters, AM W20341, HUJ).

Aruba: 9. Spaans Lagoen, SE of bridge, rocks, etc., at floodgate, mud, *Rhizophora*, 0-2.0 m, legit P. Wagenaar Hummelinck, 24.iii.1970, Stn.1673 (2 specimens BM(NH) 1992.12-13). 10. Andicuri, cape W of beach, windward side, rockpool, exuberant coral growth, strong wave action, 0.5 m, legit H. A. ten Hove, 20.viii.1970, Stn.2034B (several fragments of tubes, 2 incomplete worms, ZMA V. Pol. 3719).

Barbuda: 11. Great Lagoon, Lobster Point, N. of Palm Beach, *Thalassia* and *Halophila*, 0-1.0 m, legit P. Wagenaar Hummelinck, 23.vii.1967, Stn.1534 (3 out of several specimens, ZMA V. Pol. 3725).

Bonaire (Neth. Ant.): 12. Lac, dam, beachrock in current behind surf, 5-10 cm, from crevices in beachrock, legit H. A. ten Hove, 15.vii.1970, Stn. 2123 (1 specimen, USNM 130986). 13. Lagun, N shore, 500 m from entrance, rock, boulders, 0-50 cm, from undersides of boulders, legit H. A. ten Hove, 23.vi.1970, Stn. 2129 (3 out of several specimens, ZMAV. Pol. 3720). 14. Bonaire, Karpata, reef, 10 m, cryptic, legit H. A. ten Hove, 9.xi.88 (1 tube, BM(NH) 1992.14).

Jamaica: 15. Drunkeman's Key, sandy debris, 0-0.5 m, legit P. Wagenaar Hummelinck, 15.vi.1973, Stn.1683, (ZMA V. Pol. 3723).

Puerto Rico: 16. La Parguera, E, glade in mangroves, *Thalassia* beds, muddy sand, from between boulders, 20-30 cm, legit H. A. ten Hove, 1.x.1970, Stn.2135 (3 specimens, ZMA V. Pol. 3724).

Panama: 17. Gatun Locks, walls of outer platform, lower W chamber, Pan. Survey, 20.iii.1972, Pacific Stn. 81-1, M. L. Jones coll., USNM No.58661 (2 specimens without their tubes). 18. Same, Stn.81-2, M. L. Jones coll., USNM No.58662, (1 specimen with its tube).

Florida: 19. Safe Harbour, Stock Island (near Key West), Florida Keys, 5 m, from chunks of calcareous materials (shells, barnacles, etc.) cemented together and covered with serpulids and small cirratulids, legit R. Chesher and C. Hamlin, 17.vii.1970 and 1.vi.1971, Stn.7B, (22 out of several specimens, USNM 130988, BM(NH) 1992. 15-19, ZMAV. Pol. 3721 (10+ specimens from 1.vi.1971). 20. Off Egmont Key, 27. 0°37.0'N, 83°01.5'W, sea buoy, 18 m, scarce sponges and corals, 2 cm of soft sludge on limestone, many serpulids, legit H.A. ten Hove and T. Perkins, 2.i.1980, Stn.EJ.80002, (9 out of several specimens, ZMA V. Pol. 3722, FSBC I 39202).

TYPE LOCALITY. Curaçao (Netherlands Antilles).

DESCRIPTION.

TUBES: Light to bright pink or rose coloured. They form mutually bonded aggregations of a few to several individuals. Their external diameter is generally about 1.0 mm, maximally 1.5 mm. There are three longitudinal ridges, one median and one along each lateral margin, which may be

indistinctly developed in places (Figs.14, A; 15, A). Narrow transverse ridges may be developed to various extents (Fig.15, A). Some of the tubes end anteriorly in 4 rounded, anteriorly-directed lobes. A transparent to translucent granular overlay is present. The granulations are larger and more densely laid along the ridges. The pink colour is faint along the longitudinal ridges, as seen through the transparent granules, but form of a pair of bright longitudinal bands between the ridges. Branching tubes, difficult to observe since they form dense aggregations, have been observed in material from Curaçao (Stn. 2090, 2096, 75-38), and from Bonaire (Stn. 2123).

ITS consist of a serrated ventral ridge along the concave wall (Figs.14, B,D; 15, P), and a smooth dorsal ridge opposite (Figs.14, B, D-F; 15, O,P). The dorsal ridge is nearly tongue-shaped in cross-section, with a gradual decrease of its height, thickness and width of the widest part both anteriorly and posteriorly. This is occasionally more clearly seen in the non-coiled portions of tubes (Fig.14,F). The dorsal ridge may be situated on a columella-shaped axis in tubes coiled upon themselves (Fig.14, E). They usually also possess a short accessory dorso-lateral ridge on either side of the dorsal ridge (Figs.14, B & C; 3, L). The inside of the tube may have a light caramel to light brown lining. The mid-ventral and mid-dorsal longitudinal abdominal grooves of the worm are applied to the serrated ventral and smooth dorsal ridges, respectively.

WORMS: The longest available complete worm is from Florida. It has a total length of 12.8 mm, thoracic width of 0.5 mm, abdominal length of 9.7 mm, and has 91 segments, with capillaries commencing on the 80th. There are four radioles and a rudimentary operculum on each side. Fully developed opercula are absent in all the specimens, being represented by a long and filamentous rudimentary operculum on each side (Fig.14, H). The highest number of radioles is 6 pairs, the longest measure about 2.1 mm, and end in slender pinnule-free tips which are 1/5-1/6 their entire length (Fig.14, H). Radioles have up to 12 pairs of pinnules each, as could be observed in living material. The smallest worm is a juvenile from Curaçao (Stn. 75-77) which has a total length of 3.7 mm, a thoracic width of 0.45 mm, abdominal length of 2.0 mm, and has 20 segments, with capillaries in the last 5. It has 4 radioles on the left and 5 on the right, in addition to the rudimentary opercula.

Two reddish to reddish-brown clusters of prostomial ocelli are present. The median lobe of the collar is sub-rectangular, with rounded lateral borders and a smooth medial notch (Fig.14, I & J). Five to seven globular ventral thoracic glands are present (Fig.14, G), more or less arranged in a V. Whether they are responsible for secreting the brownish inner lining of the tube or not has to be further investigated.

A summary of data is presented in Table 13. Similar data from the Florida material are provided in Table 14.

The bayonet collar chaetae, which number 3 or 4 fully formed ones per fascicle and, usually, a developing one deep within, are unique among the species of *Spiraserpula* and of *Serpula* that have hitherto been described. Their blades are conspicuously short, unserrated and dagger-shaped (Figs.14, K-M; 15, B-I, Q-W; Pl.4, E & F). The number of large conical teeth on the basal boss is usually 3 or 4. Often there are 2 large teeth with 1 or 2 smaller ones in between (Fig.14, K-L; 15, B-I). In the specimens from Gatun Locks, Panama, the number of teeth is usually 4 or 5 (Fig.15, Q-W). These dagger-shaped bayonet chaetae were noted and figured in the

Table 13 *S. caribensis* sp. nov. A summary of data from four samples from Curaçao (Stns. 75-38, 75-36 and 75-77 and 2096).

No. of specimens (n=10)	2	7	1		
No of radioles per side	6/5	5/5	5/4		
No. of specimens (n=14)	2	1	3	3	4
No. of thoracic chaetal tufts	9/8	9/7	8/8	8/7	7/7
No. of specimens (n=10)	1	2	4	2	1
Thoracic membrane ends	5/4	5/3	4/4	4/3	3/3

Table 14 *S. caribensis* sp. nov. A summary of data from the Florida material.

No of specimens (n=11)	2	5	4		
No of radioles per side	6/6	5/5	4/4		
No. of specim.(n=29)	1	8	1	3	6
No. of thor. chaet.	10/6	9/8	9/7	8/8	8/7
				8/6	7/7
				7/6	7/5
				6/6	
No. of specimens (n=26)	3	3	4	9	7
Thor. membranes end on	5/4	5/3	4/4	4/3	3/3

unpublished research of M. van Vliet and R. Fijn (see acknowledgements).

The blades of developing bayonet chaetae deep within the fascicle are similar to the fully formed dagger-shaped bayonet chaetae, indicating that the latter have not resulted from wear and tear of bayonets with tapered tips. Occasionally, a developing chaeta with a truncated blade and tapered tip (Fig.15, F,S), occurs deep within a fascicle, which provides a clue to the origin of the former. Reduction in length of the blade together with extension of the unserrated notch has resulted in stout, truncated bayonet chaetae, with smooth and dagger-shaped blades.

Thoracic uncini (Fig.15, J) usually possess 6 teeth, and anterior abdominal uncini (Fig.15, K,X) 4 or 5, in a single row. Posterior abdominal uncini are rasp-shaped (Pl.5, A). Flat trumpet chaetae number up to about 5 in each bundle, and their triangular distal ends bear a hook-shaped process on one side, and the other side is drawn out into an acute angle (Fig.15, L-N, Y; Pl.5, B).

COLLECTIONS FROM OTHER LOCALITIES. The specimens from the other localities listed above agree with those from the type locality. However, the smaller size of the tube and chaetae of the specimens from Gatun Locks, Panama, and the highly branched tubes of the specimens from Grenada, are worth noting.

LIVE MATERIAL. As observed in material from Curaçao, radioles are colourless, transparent to transparently orange, sometimes with reddish pinnules. Base of branchial lobes and the collar may be tinged with purple. Branchial eyes not

present. Body predominantly transparent orange, thorax ventrally reddish.

ETYMOLOGY. The name acknowledges the fact that this appears to be the most widely distributed species of *Spiraserpula* in the Caribbean.

HABITAT AND DISTRIBUTION. *S. caribensis* inhabits shallow water, intertidally down to a few metres in the Caribbean, to 18 m in the E. Gulf of Mexico (temperature submerged ?). It occurs in a variety of habitats, from rockpools to the under-sides of boulders in mangrove glades. It is able to survive well in somewhat muddy environments, always, however, cryptic between piles of rock or similar hard substrata.

It appears to be widely distributed in the Caribbean and Gulf of Mexico, from Florida to Barbuda and Panama.

A population from Grenada, with frequently branching tubes and which is, for the present, regarded as belonging to *S. caribensis*, is described below (Fig.16, A-K):

MATERIAL EXAMINED.

Grenada (Caribbean), Hog Island, near Pt. Salines, 0-1.5 m, *Rhizophora*, mud, legit P. Wagenaar Hummelinck, 8.vii.1967, Stn. 1550 (5 specimens and 4 tubes, ZMA V.Pol. 3706, USNM 130985, BM(NH) 1992.32).

DESCRIPTION.

TUBES: Dark pink to rose coloured. Except for their posterior ends, they are all uncoiled, conspicuously branched, and attached to the substratum throughout (Fig.16, A). A granular overlay is present, larger granules constituting a median longitudinal ridge and a pair of lateral ridges (Fig.16, A,B). The colouration is darker pink between the median and lateral ridges. Fine transverse ridges may be present in places. The lumen of the tube is continuous with that of the branches.

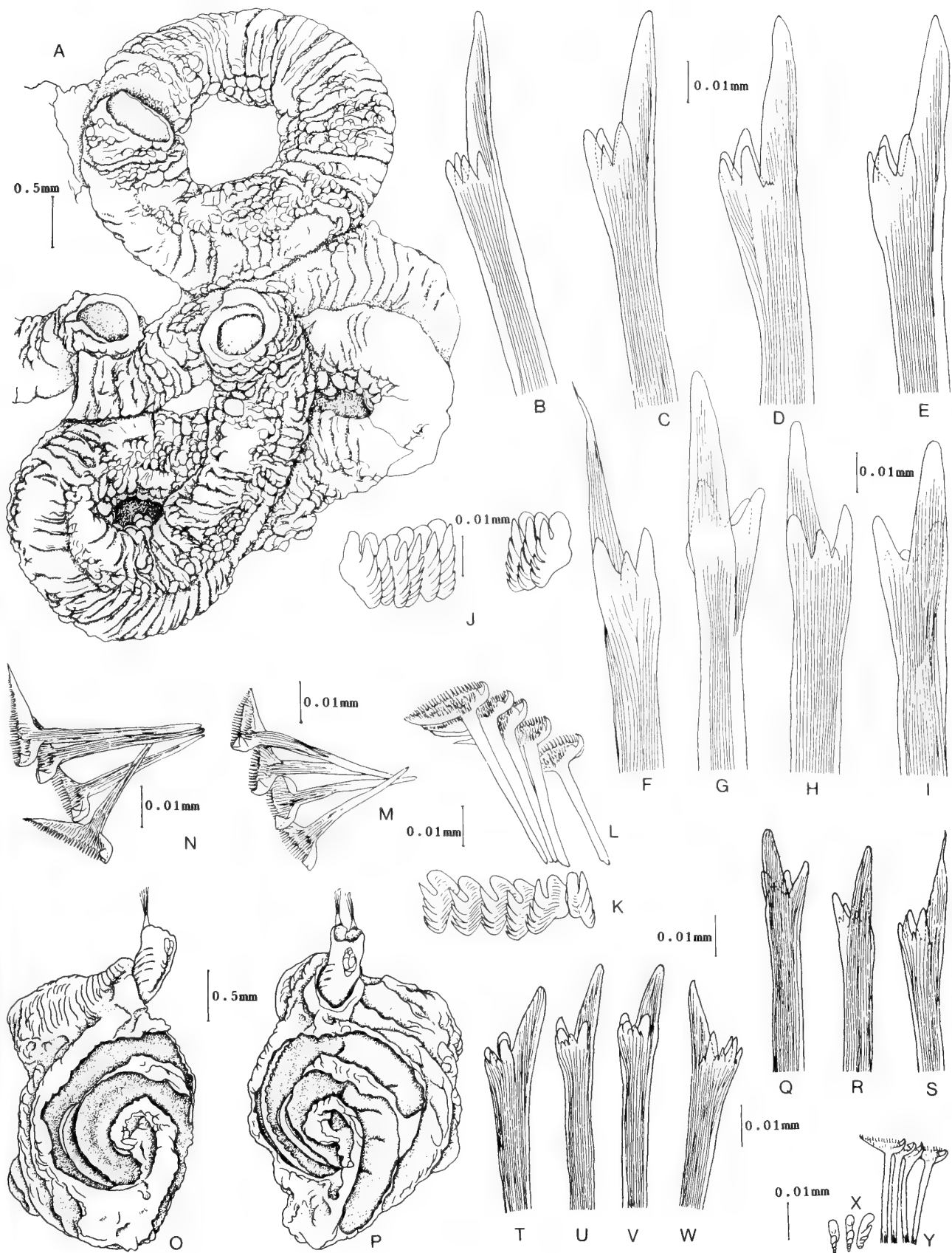
ITS are similar to those of *S. caribensis*. However, the tongue-shaped cross-section of the dorsal ridge is somewhat more pronounced.

WORMS: Three worms were taken out of the tubes, of which the longest (Fig.16, C,D), has a total length of 9.2 mm. There are up to 5 pairs of radioles and a rudimentary operculum on each side. The radioles are up to about 2.0 mm long, 1/6-1/8 of which constitute pinnule-free tips. Measurements and meristic data are given in Table 15:

Two clusters of prostomial ocelli are present. All three specimens bear 7 thoracic chaetal tufts on the left and 6 on the right. The thoracic membranes end on the third thoracic chaetiger on both sides in the first specimen, but are damaged in the others. A pair of ventral thoracic glands is present (Fig.16, C).

Each bayonet chaeta typically consists of a short, serrated blade, and an unserrated notch and a tapered tip (Fig.16, E-K). There are 2 or 3 large teeth on the basal boss, and a few accessory teeth. Older chaetae in a fascicle which have

Fig. 15 *Spiraserpula caribensis* sp. nov. A-E & J-N, From Curaçao, St. Jorisbaai, Stn. 2096. F-I, from Curaçao, Lagoen Blancu, Stn. 75-36. O-Y, From Panama, Gatun Locks: (O-S, from Stn. 81.1; T-Y, from Stn. 81.2). A, Tubes showing granular overlay, external ridges and transverse wrinkles. B-E, Bayonet chaetae from the same fascicle with short dagger-shaped blades. F-I, Bayonet chaetae from fascicle of another specimen: F, Newly formed, deep within fascicle; G-I, Older chaetae. J, Thoracic uncini. K, Anterior abdominal uncini, and L, flat trumpet chaetae, from same segment. M & N, Flat abdominal trumpet chaetae from other specimens. O & P, Tube opened sublaterally, viewed from two different angles, with worm in situ showing thoracic glands; O, with dorsal ridge only, and P, with both dorsal and ventral ridges. Q-S and T-W, Bayonets from two different fascicles. Note much smaller size compared with those of Florida (Fig. 14, K-L) and Curaçao (Fig. 15, B-I) material, although drawn under same magnification. X & Y, Anterior abdominal uncini and flat trumpet chaetae from same segment. Note much smaller size than in Curaçao material (Fig. 15, L-N). •



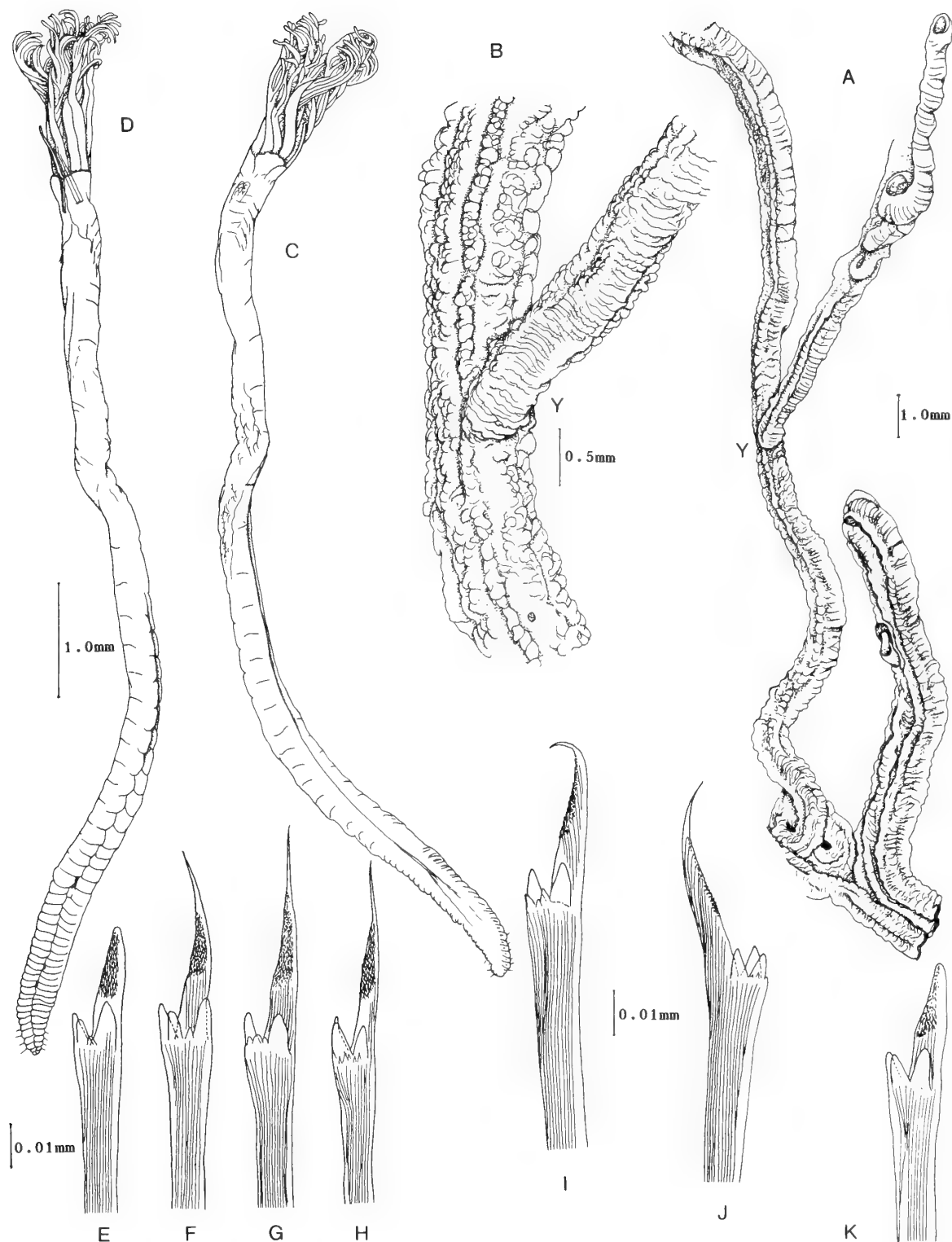


Fig. 16 *Spiraserpula caribensis* sp. nov. A-K, From Grenada. A, Branched tube with granular overlay and longitudinal ridges. B, Branching point marked Y in A, magnified. C & D, Two views of a worm showing rudimentary opercula, thoracic glands (C), and dorsal and ventral longitudinal abdominal grooves. E-H, Four bayonets from a small specimen: A, Older chaeta with worn out tip; F-G, Chaetae with intact tips. I-J, Bayonets from a larger specimen: the oldest (K) with a worn out tip, and the other two with intact tips.

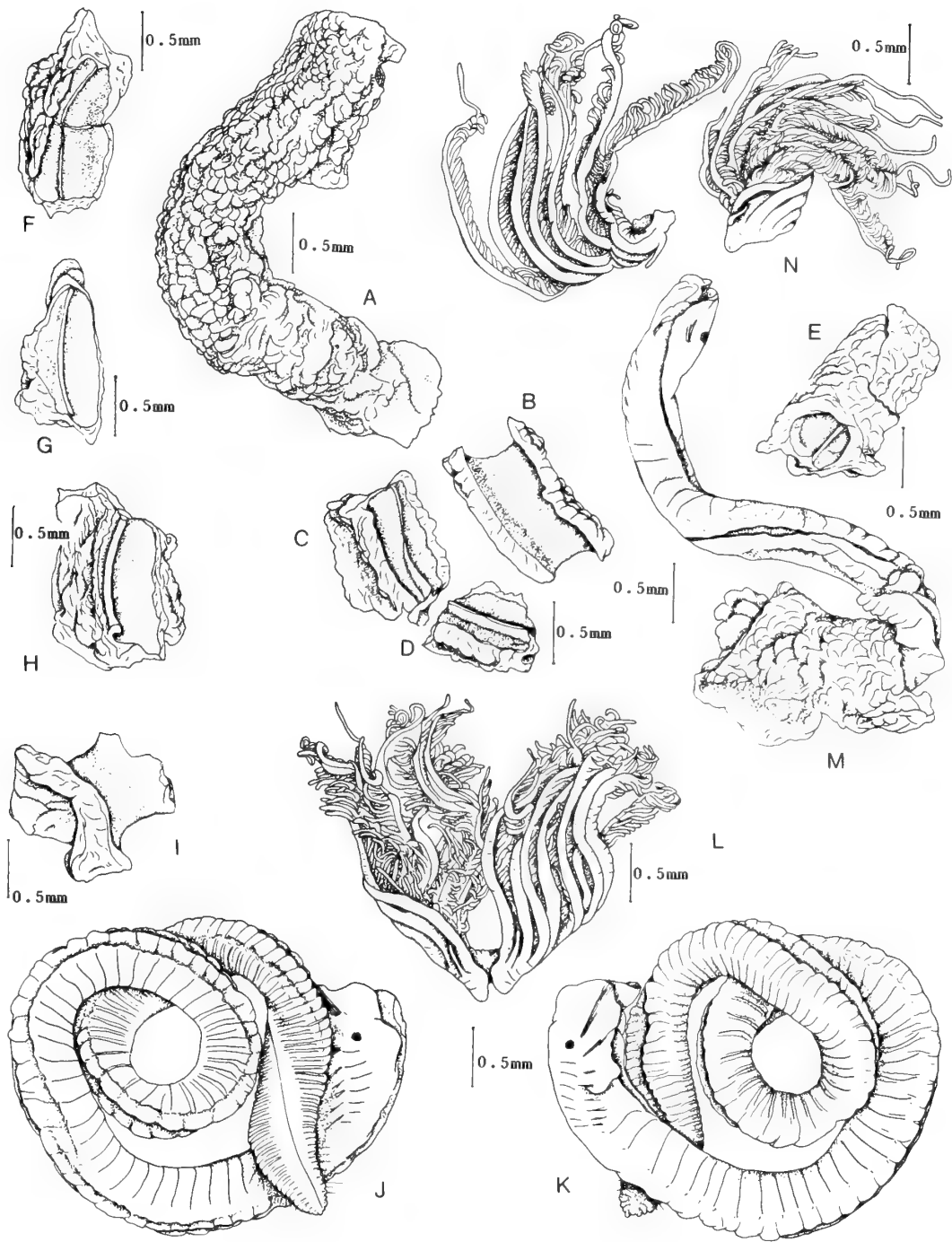


Fig. 17 *Spiraserpula nudicrista* sp. nov. From Bonaire. A, Tube, with granular overlay and longitudinal ridges. B-D, Tube fragments showing unserrated ventral ridge along concave wall and lack of a ridge on the opposite side. E-I, Other tube fragments showing a narrow ventral ridge anteriorly, and a smooth and rounded edge to it posteriorly. J, First formed coil, lacking a dorsal ridge. K-L, Two different views of holotype showing prostomial ocellar clusters, as seen through the collar, the ventral longitudinal groove of the abdomen, and extent of thoracic membrane on the left side (K); L, Radioles with a pair of short club-shaped rudimentary opercula and moderately long pinnule-free tips. M & N, Paratype: M, tube with granular overlay, prostomial ocellar cluster of one side, and longitudinal abdominal grooves; N, branchial crown with a pair of short club-shaped rudimentary opercula, and long pinnule-free tips.

Table 15 *S. caribensis* from Grenada. Measurements and counts.

Specimen no.	Total length (mm)	Thoracic width (mm)	Radioles		Abdomen		Capillaries on
			Length (mm)	Length No. (mm)	Number of segments		
1	9.2	0.5	2.0	5/5	6.6	50	44
2	8.1	0.5	1.2	4/3	4.7	30	7
3	3.1	0.35	0.6	3/3	1.8	35	10

lost their tapered tips through abrasion may appear somewhat like the bayonets of *S. caribensis* from elsewhere (Fig.16, E, K; Pl.5, C-E), but the newly formed bayonets, within the fascicle, possess tapered tips.

HABITAT AND DISTRIBUTION. Appears to inhabit shallow water and capable of withstanding the silty conditions found in mangrove backwaters. It was found on the inside of a dead oyster shell covered with much silt.

REMARKS. The extensively branching tubes and differences in the collar chaetae initially led us to consider the Grenada material as possibly belonging to a distinct species. However, branching as such, although inconspicuous, was also subsequently observed in some specimens of *S. caribensis* from Bonaire (Stn. 2123) and Curaçao (Stns. 2090, 2096, 75-38; see above), in *S. parapsylon* from Curaçao (10.i.90). Moreover, *S. snellii*, described later in this paper, revealed a schizont with parent in one tube. By itself, therefore, branching cannot be a good character to separate the Grenada material as a distinct species. The fully formed bayonet chaetae, including those within the fascicle, of *S. caribensis* proper, have short dagger-shaped blades with blunt tips, while blades of the Grenada material typically end in tapered tips. Although the tip of a fully formed chaeta in the Grenada material might be lost through abrasion (Fig.16, E-K), those deep within the fascicle are tapered.

Further work on additional material is necessary to determine whether frequent branching of the tubes and the features of the bayonet chaetae are consistent, and whether there are other characters which would justify the separation of the Grenada material into a distinct species or not.

Spiraserpula nudicrista sp. nov.

(Figs.17, A-N; 18, A-O; 3, F; Pl.3, A-D)

MATERIAL EXAMINED.

Bonaire (Neth. Ant.): 1. Karpata, reef, cryptic, 10 m, legit H. A. ten Hove, 9.xi.1988, (HOLOTYPE & PARATYPE: ZMA V. Pol.3711).

Curaçao (Neth. Ant.): 2. Savonet, E of Boca Braun, reef, no sand, about 22 m, from corals, some dead, legit H. A. ten Hove, 28.xi.1970, Stn. 2101 (PARATYPES 2 & 3: BM(NH) 1992.61 & 62).

TYPE LOCALITY. Bonaire (Netherlands Antilles).

DESCRIPTION.

TUBES: White to creamish white and have a conspicuous granular overlay (Fig.17, A,E,M). They may be covered over by encrusting calcareous organisms. They are trapezoidal in cross-section, with two longitudinal ridges along the crest of the tube and one along each flank (Fig.17, A). The maximum external tube diameter of the holotype is 1.0 mm.

ITS consist of an unserrated ventral ridge which is rounded and smooth towards its middle (Figs.17, H; 3, F), from where it decreases in thickness and height both anteriorly and posteriorly (Fig.17,C-E, F-G). A dorsal ridge is generally absent, even on the convex pulley-shaped posterior end (Fig.17, I). However, paratype 1 from Bonaire showed some isolated dorsal teeth. The mid-ventral longitudinal groove of the abdomen (Fig.17, M) is applied to the unserrated ventral ridge.

WORMS: Only two worms were yielded by the tubes from Bonaire. The complete holotype has a total length of 15.6 mm, a thoracic width 0.7 mm, an abdominal length 11.9 mm and about 101 segments, with capillaries on the last 7. The radioles are 2.5 mm in length, and their pinnule-free tips of 0.6 mm are comparatively long (Fig.17, L, N). The paratype is incomplete posteriorly.

The holotype has 9 pairs of radioles while the paratype has 8 pairs. Both specimens have a short filamentous rudimentary operculum on each side (Fig.17, L). Two clusters of prostomial ocelli are present, and are seen as conspicuous brown patches through the collar (Fig.17, J,K,M). This is in contrast to the other known members of the genus in which they can be seen when viewed from the anterior end with the radioles removed or when mounted.

Both specimens have 8 pairs of thoracic chaetal tufts, and the thoracic membranes end on the fourth chaetiger on the left (Fig.17, K) and the 5th on the right. Ventral thoracic glands appeared to be absent.

The collar fascicles of the holotype possess four bayonet chaetae with long serrated to pilose blades and several conical teeth on the basal boss (Fig.18, A-D; Pl.3, A). There may be a number of accessory teeth arranged around the bases of the larger teeth, which are lacking in the paratype (Fig.18, E-G). The unserrated notch is short. Thoracic uncini (Fig.18, H; Pl.3, B) and anterior abdominal uncini (Fig.18, I; Pl.3, C) possess 4 or 5 teeth arranged in a single row. There are about 4 flat trumpet chaetae in each abdominal fascicle (Fig.18, J; Pl.3, D). An anterior hook, as in most of the species of the group, cannot be discerned, all distal teeth appearing more or less equally developed.

Tubes of the specimens from Curaçao are similar to those from Bonaire with regard to colour, form and ITS (Fig.18, K). Their maximum external diameters are 1.1-1.2 mm. Two of them yielded worms which are incomplete posteriorly. Some data from them are presented in Table 16.

Both specimens possess a rudimentary operculum on each side (Fig.18, L,M). Bayonet collar chaetae (Fig.18, N,O), are similar to those of the specimens from Bonaire, although their basal bosses are somewhat stouter.

REMARKS. A small fragment from the inside of the coil of

Fig. 18 *Spiraserpula nudicrista* sp. nov. A-J, From Bonaire. A-D, Bayonet chaetae, holotype. E-G, Three, out of five, bayonet chaetae from paratype. H-J, from paratype: H, Thoracic uncini; I & J, flat trumpet-shaped chaetae and uncini from anterior abdomen. K-O, From Curaçao. K, Tube, with granular overlay, external longitudinal ridges, and internal ventral longitudinal ridge seen through fractured end. L, Branchial crown of older specimen with pair of rudimentary opercula. M, Branchial crown of younger specimen, with pair of shorter rudimentary opercula. N & O, Two, out of four, bayonet chaetae.

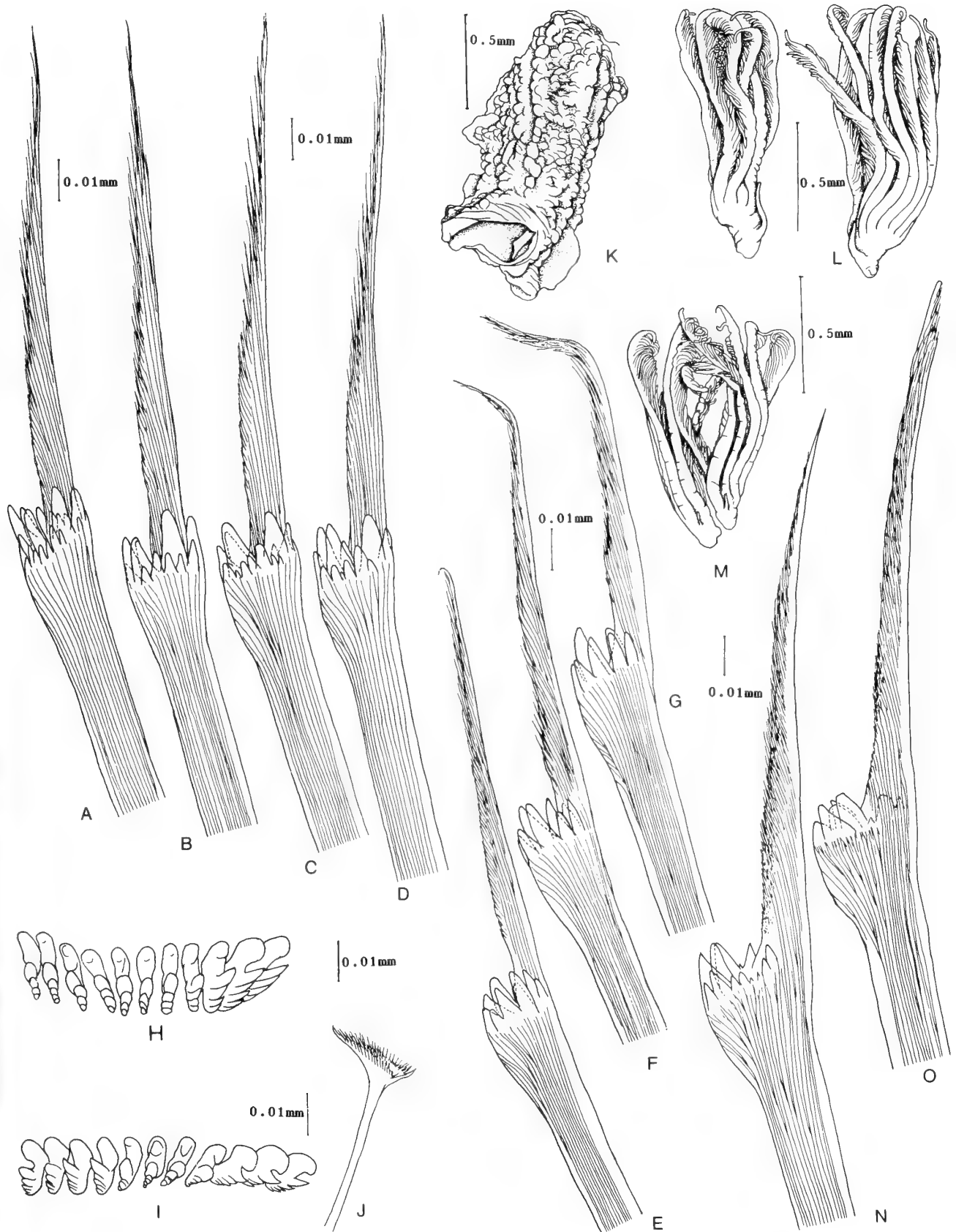


Table 16 *S. nudicrista* sp. nov. Some data on two specimens from Curaçao.

	Specimen 1	Specimen 2
Width of thorax	0.5 mm	0.6 mm
Length of radioles	2.1 mm	2.6 mm
Pinnule-free tips (Figs.17L,M)	short	short
No. of radioles (L/R)	7/8	9/8
No. of thoracic chaetal tufts (L/R)	9/7	8/6
Thoracic membrane ends	??	4/4
Length of abdomen	?	9.7 mm
No. of abdominal segments	?	about 60

paratype 1 showed a slightly concave to asymmetrical cross-sectional edge to the ventral ridge, and a few isolated teeth in the location of the dorsal ridge, somewhat similar to the condition in *S. parapsilon*. There is also some similarity in the collar chaetae.

ETYMOLOGY. nudus (L) = unadorned; crista = crest, ridge.

HABITAT AND DISTRIBUTION. *S. nudicrista* is a shallow water cryptic species inhabiting coral reefs. It has hitherto been collected from Bonaire and Curaçao.

***Spiraserpula* sp.**
(Fig.19, A–C)

MATERIAL EXAMINED.

Curaçao (Neth. Ant.): Piscadera Baai, outer bay in front of CARMABI, muddy reef, many sand spots, about 40 m, from dead corals, legit H.A.ten Hove, 9.vi.1970, Stn. 2054B (3 empty tubes, and some abdominal fragments, ZMA V. Pol. 3883).

DESCRIPTION. Tubes are white, circular in cross-section. An

erect portion shows a granular overlay, and an encrusting sponge at its base (Fig.18,A). ITS characteristic of this genus are present in the coiled parts, and consist of an unserrated dorsal ridge and a serrated ventral ridge. The dorsal ridge is transparent, somewhat high, and has a smooth, somewhat T-shaped edge; it is spiral, on a columella-shaped axis in the spiral proximal portions of the tube (Fig.18, B,C). The available portions of the worms were inadequate to assign the material to any of the other Caribbean species or a new species.

***Spiraserpula vasseuri* sp. nov.**
(Figs.20, A–H; 21, A–K; 3, J)

Helmut Zibrowius requested (pers. comm.) that the material on which he based his preliminary description of the present species in an unpublished manuscript be examined, and that it be included in this paper if it belonged to the present group. ITS are indeed present in this species, and its description follows:

MATERIAL EXAMINED.

Europa Island (Mozambique Channel): North Reef, Gabriel Cove grotto, 55 m, on oysters, legit Pierre Vasseur, scuba diving, 28.xii.1965 (HOLOTYPE: USNM 46475, 6 PARATYPES USNM 46476).

TYPE LOCALITY. Europa Island.

DESCRIPTION.

TUBES: The colour is mostly whitish, with a very faint pinkish to orangish tinge seen in places at certain angles of illumination. They are sinuous, coiled and bonded together, especially at their bases. A granular overlay is present. The anterior portions are squarish to trapezoidal in cross-section (Fig.20, A–C). The dorso-lateral angles may be incompletely developed in places and represented by a pair of incomplete longitudinal ridges; an additional incomplete ridge may be

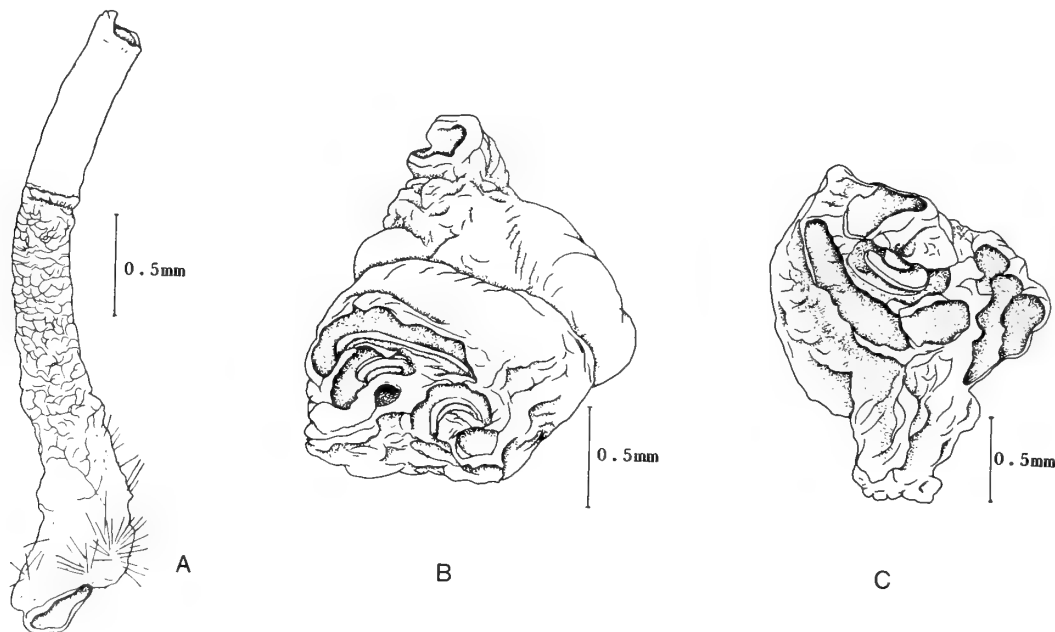


Fig. 19 *Spiraserpula* sp. A–C. Three specimens from Curaçao. A, Erect part of tube with encrusting sponge on its base. B, A tube opened to show spiral dorsal ridge in its first formed coil. C, Aggregation of tubes opened to show variations of dorsal ridge.

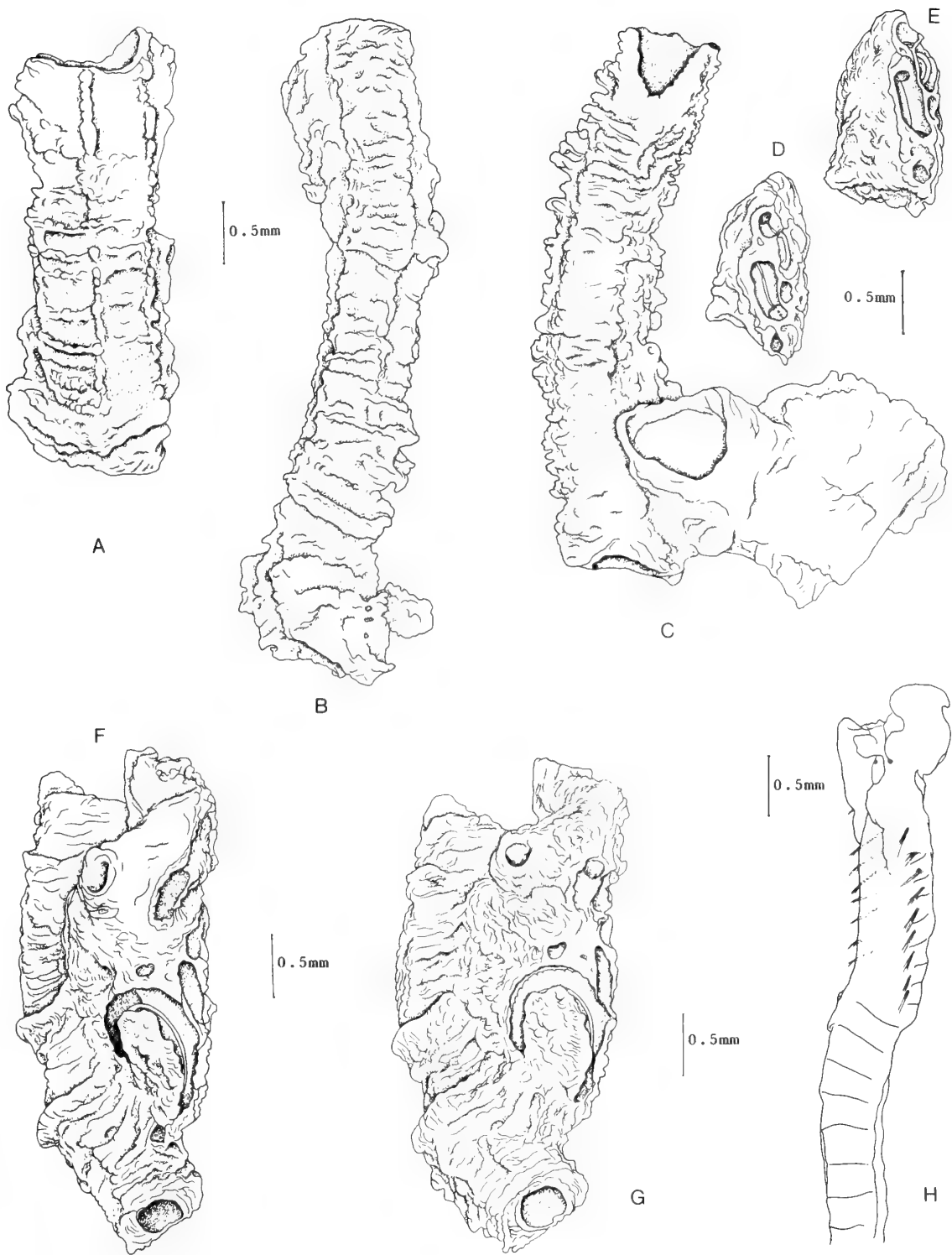


Fig. 20 *Spiraserpula vasseuri* sp. nov. A-H, paratypes. A-C, Anterior tube fragments showing granulations, transverse ridges and roughly trapezoidal external outline. A, Shows incompletely formed external longitudinal ridges, and a thickened peristome towards the posterior end of B. D & E, Two views of same posterior coil showing the unserrated dorsal ridge in both, and a serrated ventral ridge consisting of separate teeth in D. F & G, Two views of same anterior tube fragment with an attached posterior coil opened (on the right). The anterior tube fragment has two peristomes; the posterior coiled part (G) has been opened to expose the unserrated dorsal ridge and serrated ventral ridge (G). H, Thorax showing prostomial ocelli, collar, thoracic membranes and chaetigers.

present along each flank (Fig. 20, A). Transverse ridges are present, which may be thickened in places, representing peristomes (Fig. 20, B, F, G). Although broken into fragments during collection, total lengths appear to have been between 30–40 mm, and their maximum external diameters up to about 3.0 mm. Their fractured ends show two concentric layers of different consistency and thickness, an inner one that is more vitreous and transparent than the outer which is white and opaque. Their lateral margins are fragile and chambered, with thin walls.

The posterior ends of the tubes are coiled. ITS consist of a low unserrated dorsal ridge, and a serrated ventral ridge (Fig. 20, D–G). The latter may be represented by a row of separate teeth (Figs. 20, D; 3, J).

WORMS: The total length of the worms, based on the fragments, exceeds 15.0 mm. The branchial crown is 4.0–5.0 mm long, and each side bears 8–10 radioles and an operculum or a rudimentary operculum. The opercular peduncle is long and slender, of the same thickness as the radioles. One of the specimens has a well-developed operculum on one side, and another, much smaller, but similar operculum on the other. The operculum is big and short, massive, bell-shaped, and slightly concave distally. The radii end in large, rounded marginal lobes, and range from 10 to 15 in number (10 in 1, 11 in 3, 12 in 1, and 15 in 1). The number of thoracic segments per side varies from 10 to 14. A pair of small ocellar clusters is present. Collar large, roughly divided into three large ventral lobes and a pair of latero-dorsal lobes. Thoracic membranes are broad up to the third segment, after which they narrow, and do not form an apron.

The longest opercular peduncle (holotype) together with its operculum is 5.5 mm long. The operculum (Fig. 21, A, C, D) is separated from the peduncle by a faint constriction, where the peduncle is only 1/2–1/3 the diameter of the base of the operculum. The variations in the dimensions of opercula of the older specimens are as follows: length: 0.6–0.7 mm; width: 0.55–0.6 mm. They are bell-shaped, with a small shallow concavity distally. They have a thick and transparent cuticle (Fig. 21, A, C, D). The second radiole of the opposite side is modified into a rudimentary operculum (Fig. 21, B). The radioles end in short pinnule-free tips which are about 1/10–1/15th the total length of the radioles (Fig. 21, A–C).

One of the specimens, a juvenile, provides an indication of the possible ontogenetic changes in the operculum of this species. Unlike in the adults, where peduncle and operculum are markedly separated from each other, the slender peduncle of the juvenile merges gradually into the base of the operculum. In addition, the shape of the latter is an elongated funnel, and its distal end is convex (Fig. 21, E).

The collar fascicles may bear up to about 5 fully formed bayonet chaetae and one developing deep within. Each possesses a long serrated blade, a short unserrated notch, and several moderately large teeth on the basal boss (Fig. 21, F–K). Thoracic uncini show 5–6 teeth in side view; however, in oblique edge view it is evident that they are saw-rasp shaped, with an anterior single row and a posterior cluster of teeth (Fig. 21, L). This is more clearly seen in the anterior

abdominal uncini (Fig. 21, M). In side view, the number of teeth in the latter vary from 4 or 5 towards the lateral end of the torus to 7 at the dorsal end. Flat trumpet chaetae number 9–11 per bundle. Their distal ends terminate in a slender hook-shaped process on one side and are drawn out into an acute angle on the other (Fig. 21, N).

ETYMOLOGY. As suggested by Zibrowius (pers. comm.), the species is named after its collector, P. Vasseur.

HABITAT AND DISTRIBUTION. A reef dweller found on oyster shells in submarine caves at depths of around 55 m. Hitherto collected only from the Mozambique Channel.

Spiraserpula deltoides sp. nov.
(Figs. 22, A–N; 3, C)

MATERIAL EXAMINED.

Lesser Sunda Islands, Sumba (Indonesia): Snellius II 4.051, NE coast of Sumba, E. of Melolo 09°53.5'S 120°42.7'E, 75–90 m. (HOLOTYPE & 1 PARATYPE (empty tube): RMNH 18296; 3 PARATYPES: ZMA V. Pol. 3736; 2 PARATYPES: BM(NH) 1992.37 & 38).

TYPE LOCALITY. Sumba (Indonesia).

DESCRIPTION.

TUBES: White, small, and spirally coiled upon themselves. They are squarish in cross-section, smooth and rounded dorso-laterally, and with a shallow longitudinal depression in between (Fig. 22, A). They have an extremely fine granular overlay, which can only be seen at certain angles of illumination, and very fine transverse grooves. The coil diameter is generally about 3 mm, maximally 9 mm; the maximum external tube diameter is generally 0.7 mm, maximally 1.3 mm. In two of the tubes an inner transparent lining was observed.

ITS consist only of a serrated dorsal ridge along the convex wall of the tube (Figs. 22, B, C; 3, C). The serrations are delta-shaped, mostly separate, and opaquely white in colour. **WORMS:** The holotype (Fig. 22, D) is 5.0 mm long, 0.35 mm wide in the thorax and its abdomen is 3.2 mm long. One paratype is incomplete posteriorly, the other is 8.0 mm long, with an abdomen of 3.5 mm. Some measurements and counts are given Table 17:

The operculum is bell-shaped, with a shallow distal concavity extending inwards as far as the inter-radial grooves. The radii end in rounded marginal lobes, the constriction between operculum and peduncle is sharp, and the diameter of the distal end of the peduncle is about 1/2–3/4 that of the proximal part of the operculum (Fig. 22, D–G). The rudimentary operculum is 1.5 mm long, thread-shaped. The radioles end in short pinnule-free tips, about 1/7 the total length of the radioles. Two clusters of prostomial ocelli are present. It is difficult to determine whether ventral thoracic glands are present. Thoracic membranes do not extend to the end of the thorax, but exactly where they end cannot be located, it may be at the 7th chaetiger in one paratype. The abdomen of the holotype has about 67 segments, with capillaries on the last 8 or 9; the complete paratype has 85 abdominal segments, 24 with capillaries. The abdomen of the incomplete paratype is

Fig. 21 *Spiraserpula vasseuri* sp. nov. A, Holotype. B–N, Paratypes. A, The left branchial crown and three views of the operculum and its slender peduncle. B, Left branchial crown and rudimentary operculum from another specimen. C & D, Branchial crowns and different views of the opercula of two other specimens. E, Two views of the convex operculum of a juvenile. F–K, Bayonet collar chaetae bearing several teeth on the basal boss, and a short unserrated notch. L, Thoracic uncini, with more than one row of teeth towards their posterior ends. M, Anterior abdominal uncini. N, Bundle of anterior abdominal chaetae with flat trumpet-shaped ends.



Table 17 *S. deltooides* sp. nov. Some measurements and counts on the holotype and 2 paratypes.

	Holotype	Paratype 1	Paratype 6
Length of operculum and peduncle	0.94 mm	1.2 mm	3.2 mm
Length of operculum	0.38 mm	0.52 mm	0.48 mm
Diameter of operculum	0.44 mm	0.35 mm	0.41 mm
No of opercular lobes	22	26	22
No. of radioles (L/R)	5/6	6/6	7/7
No. of thoracic chaetal tufts (L/R)	8/7	6/8	7/7

12.5 mm long, has about 75 segments, and the latter bear reddish-brown granular material ventro-laterally.

The collar fascicles bear 2–6 bayonet chaetae. Each has a long serrated blade, a short unserrated notch, and about 2–6 teeth on the basal boss (Fig.22, H–I, L–N). Thoracic uncini bear about 5 teeth in a single row (Fig.22, J,K); anterior abdominal uncini are similar and bear 5–7 teeth.

ETYMOLOGY. The specific name refers to the delta-shaped serrations of the internal dorsal ridge.

HABITAT AND DISTRIBUTION. Found on calcareous stones at depths of 75–90 m. Hitherto collected only from Sumba (Indonesia).

***Spiraserpula sumbensis* sp. nov.**

(Figs. 23, A–U; 3, H)

MATERIAL EXAMINED.

Sumba (Indonesia): Snellius II 4.051, NE coast of Sumba, E of Melolo, 09°53.5'S 120°42.7'E, 75–90 m, (HOLOTYPE: RMNH 18297; 1 PARATYPE: ZMA V. Pol. 3737; 1 PARATYPE: BM(NH) 1992.72).

TYPE LOCALITY. Sumba (Indonesia).

DESCRIPTION.

TUBES: White to very faintly pinkish. A small species with external tube diameter only up to about 0.5 mm, and a lumen of about 0.25 mm wide. A granular overlay consisting of extremely fine granules can be seen under special illumination. Tubes are circular in cross-section and bear faint transverse wrinkles (Fig.23, A–C, O).

ITS consist of a dorsal ridge and a ventral ridge, which are both unserrated, wedge-shaped in cross-section (Fig.3, H), and partially divide the lumen into somewhat asymmetrical left and right halves (Fig.23, C,D). The two ridges are light

Table 18 *S. sumbensis* sp. nov. Measurements and counts.

	Paratype 1		Paratype 2
	Left side	Right side	
Length of op. & peduncle (mm)	1.2	1.0	1.2
Length of operculum (mm)	0.36	0.36	0.35
No. of lobes	19	21	17
No. of radioles	5	5	4/4
No. of thoracic chaetal tufts	8	8	–
Thoracic membrane ends (Fig.23,Q)	3	5	–

pink and opaque. In cross-section they consist of a lens-shaped whitish kernel in the inner hyaline tube layer; the outer tube layer is opaque.

WORMS: The holotype (Fig.23, E–G), has a total length of 7.0 mm, thoracic width of 0.26 mm, an abdominal length of 5.1 mm and 66 segments, with capillaries on the last 17. The length of the operculum plus peduncle is 1.3 mm, the length and diameter of the operculum 0.38 mm and 0.26 mm, respectively. The operculum is zygomorphic (Fig.23, E,F). It has a distal concavity which extends as far as the inter-radial grooves. The 15 radii end in somewhat acutely triangular marginal lobes with smooth tips. The peduncle is slender, but somewhat expanded before the constriction below the operculum. There are 5 radioles on each side, with the operculum on the left side and a short filamentous rudimentary operculum on the right (Fig.23, E). The short pinnule-free tips are about 1/7–1/8 the total length of the radioles. Thoracic chaetal tufts number 8 on each side. The thoracic membrane ends on the fifth chaetiger on the left, but it is difficult to determine its extent on the right. One tiny prostomial eye appears to be present on the right side, the left side is damaged. Thoracic glands could not be detected in the material.

One paratype (Fig.23, O–Q) has an incomplete abdomen. It is the first specimen encountered in this genus with two equally well-developed opercula (Fig.23, O,P). The thorax of the second paratype is missing, the remaining abdomen has 54 segments, 12 of them with capillaries. Some measurements and other data are given in Table 18:

The paratypes agree with the holotype with regard to the tube, operculum, radioles, and chaetae. The opercula are somewhat zygomorphic.

Collar fascicles bear 4 fully formed bayonet chaetae in the holotype; 3 fully formed bayonet chaetae and a newly formed one deep within the fascicle in paratype 1. Each bayonet chaeta (Fig.23,H–K, R–U) consists of a long serrated blade, a moderately long unserrated notch, which is about 1/6–1/7 the length of the blade, and several teeth on the basal boss. Thoracic uncini appear to have a row of 7–9 teeth in side view, but more than one row as seen in edge view (Fig.23,L). Anterior abdominal uncini are similar, but appear to have fewer teeth in side view (Fig.23, M). Flat trumpets number four in each anterior bundle, their curved distal ends have a poorly developed hook on one side and are comparatively elongated on the other (Fig.23, N). Capillaries occur in the posterior 12–17 chaetigers.

ETYMOLOGY. Named after the type locality.

HABITAT AND DISTRIBUTION. Found on calcareous stones at depths of about 75–90 m. Hitherto collected only from Sumba (Indonesia).

***Spiraserpula iugoconvexa* sp. nov.**

(Figs. 24, A–K; 25, A–Q; 3, I)

MATERIAL EXAMINED.

NE Flores Sea to SW Banda Sea (Indonesia): 1. **Taka Bone Rate** (Tiger Islands), Snellius II 4.139B, S of Tarupa Kecil, 06°30'S 121°8'E, depth –30 m, (HOLOTYPE: RMNH 18295; PARATYPE I: ZMA V.Pol.3735). 2. **Tukang Besi Island, Binongko**, Snellius II 4.044B, SW of Taipabu, Banda Sea, 5°56'S 123°58.5'E, down to 25 m, (PARATYPE II: BM(NH) 1992.39). **Queensland (Australia):** 3. Lizard Island, S. South Island, sloping silty reef, little coral cover, legit H. A. ten

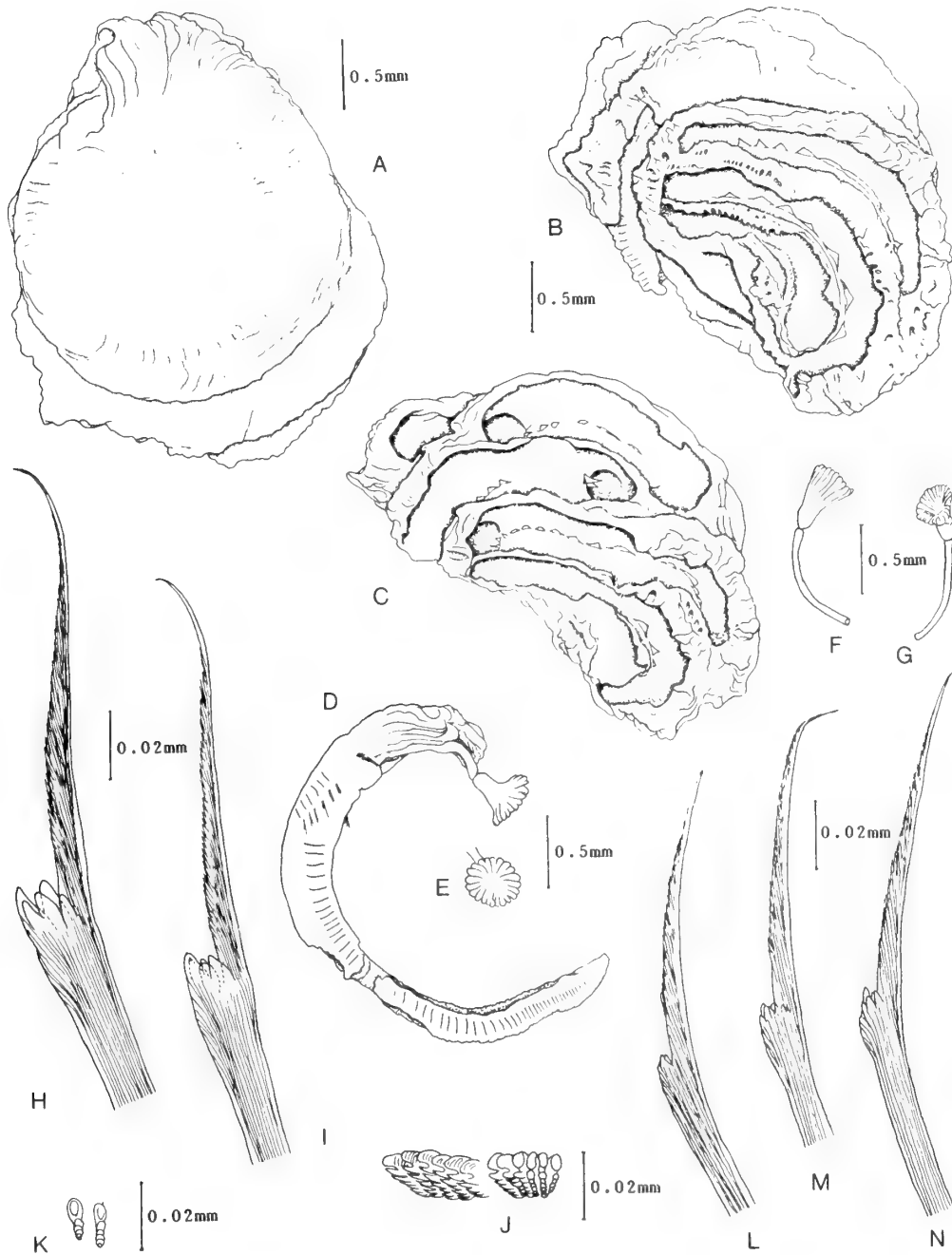


Fig. 22 *Spiraserpula deltooides* sp. nov. A-E & H-K, From holotype; F-G & L-N, from paratype. A, Tube viewed from above. B & C, Two views of same tube opened substrally to show deltooid dorsal ridge. D, Worm, showing operculum and dorsal abdominal groove. E, Anterior view of operculum. F & G, Two views of operculum. H & I, L-N, Bayonet chaetae. J, Thoracic uncini. K, Anterior abdominal uncini. L-N, Bayonet chaetae.

Hove *et al.*, Stn. 21,6.iii.1986 (1 specimen, tube; AM, W21676).

TYPE LOCALITY. NE Flores Sea (Indonesia).

DESCRIPTION.

TUBES: Bright rose, red in fresh material, with a translucent granular overlay, coiled posteriorly but not anteriorly. All three tubes of the type series were partially overgrown by encrusting bryozoans, making their surfaces irregular. At irregular intervals, there are also peculiar elongated struc-

tures with a semilunar opening, which appear to be a hydrozoan commensal, akin to *Protulophila* Rovereto, 1901 (*vide* Scrutton, 1975). These sparsely occurring structures are directed longitudinally or transversely as shown on the specimen from Stn. 4044B (bottom end of Fig.24, A). The anterior end of the tube from Tukang Besi Island is not attached to the substratum. Viewed dorsally, it is squarish to trapezoidal in cross section. It has two fairly distinct dorso-lateral ridges and a faint median one in places, transverse wrinkles which are occasionally thickened, and an expanded

peristome at its anterior end (Fig.24, A). The ventral side of the unattached part, which commences from a swollen attachment to the substratum, does not show the granular overlay but only faint transverse wrinkles (Fig. 24, B). The peristome consists of a broad triangular dorsal lobe which is continuous with two narrow ventro-lateral lobes (Fig.24, A,B). The inside of the tube is quite shiny. It attains a diameter of 1.6 mm at the peristome, and 1.5 mm at the swollen commencement of the unattached part.

ITS, which are present only in the posterior part of the tube, consist of an unserrated dorsal ridge (Figs.24, C; 25, B,C), and a very short smooth ventral ridge (Fig.3, I), which is very short in the holotype (Fig.25, D); in the specimen from Lizard Island the ventral ridge is smooth to scalloped. The dorsal ridge may be T-shaped in cross-section in places (Fig.25, C) but appears irregular if damaged (Fig.24, C, middle). In the middle region of the tube, tear-shaped depressions are present in the inner wall, up to 0.2 mm in size.

WORMS: The holotype from Taka Bone Rate, broken in three parts (Fig.25, E–G), has a total length of 31.5 mm, a thoracic width of 0.5 mm, an abdominal length of 27.0 mm and 117 segments, with capillaries on the last 8. Its radioles are 2.7–3.0 mm long, of which the slender pinnule-free tips constitute 0.3 mm. Paratype I lacks its branchial crown; it has a length of 5.0 mm, a thoracic width of 0.4 mm, an abdominal length of 4.3 mm, and has 61 segments, with capillaries on the last 15 or 16. Paratype II, from Tukang Besi Island, lacks its radioles on the right side, and its abdomen is in several parts. Its thorax, however, is intact (Fig.24, G,H).

The operculum and peduncle measure 3.0 mm long in the holotype, 4.1 mm in paratype II. Other measurements and counts are given Table 19.

The operculum is zygomorphic, and its distal end is quite different from that of other known species of the genus in being markedly convex (Figs.24, D–F; 25, G–J). The cuticle is thickened and transparent, particularly in its convex distal end, the marginal lobes of the radii, and the asymmetrical projection at the base of the operculum. The number of radial lobes reaches about a dozen. There is a sharp constriction between the operculum and the peduncle, the latter being slender, except for a slight expansion before the constriction (Figs.24, E,F; 25, J). A filamentous rudimentary operculum is present on the side opposite to that of the operculum (Fig.25, G).

The number of radioles per side reaches 14. Their short pinnule-free tips are about 1/7–1/8 the entire length of the radiole. Prostomial eyes were not found. Thoracic glands are present, transparent in the holotype and paratype II, light brown in paratype I. The number of thoracic segments per side is 7–8, and the thoracic membranes do not reach the last thoracic segment (Fig.24, G–I).

The abdomen of the holotype appears glandular ventrally, packed with eggs, and bears peculiar swellings (Fig.25, E) which fit into corresponding depressions in the tube. It was not possible to find them in the damaged abdomen of paratype II, although this is a mature specimen too, and the inner tube wall shows tear-shaped depressions (0.32×0.22 mm); they are absent in

Table 19 *S. iugoconvexa* sp. nov. Measurements and other data on type specimens.

	Holotype	Paratype I	Paratype II
Length of operculum (mm)	0.7	?	1.0
Diameter of operculum (mm)	0.5	?	0.7
No. of radii	12	?	11
No. of radioles(L/R)	10	?/?	14/?
No. of thoracic chaetal tufts	8/7	7/7	7/7
Thoracic membrane ends	?/?	1/3	5/4

the juvenile paratype I. Possibly, these abdominal swellings are developed in older worms only.

Collar fascicles of the holotype bear 4 bayonet chaetae each (Fig.25, K–N). Each possesses a long serrated blade, a short unserrated notch and two teeth on the basal boss, one of which may be difficult to observe in side view since it lies directly behind the other. The number of teeth is clearly seen in one of the bayonets of paratype I which has its blade broken off at its base (Fig.24, J), although it is difficult to observe in a newly formed chaeta from within the same fascicle (Fig.24,K). Thoracic uncini bear 5 or 6 teeth (Fig.25, O), and anterior abdominal uncini 4 or 5 teeth in a single row (Fig.25, P). There are up to about a dozen flat trumpet chaetae in each bundle (Fig.25, Q). Their distal ends bear a claw-shaped process on one side and are drawn out into an acute angle on the other.

ETYMOLOGY. *Iugum* (L) = yoke; *convexus* (L) = bulbous; refers to the zygomorphic, convex operculum.

MATERIAL FROM OTHER LOCALITY. The material from Lizard Island agrees closely with that of the type series with regard to collar chaetae, operculum and tear-shaped depressions in the inner tube wall. However, the ventral internal ridge has a scalloped edge, not smooth as in the Indonesian material.

HABITAT AND DISTRIBUTION. A reef dweller occurring at depths of about 25 m. Hitherto collected from Indonesia (Flores Sea and Banda Sea) and Australia (Queensland).

Spiraserpula snellii sp. nov.

(Figs.26, A–X; 27, A–L; 28, A–V; 3, F)

MATERIAL EXAMINED.

Flores Sea, (Indonesia): 1. **Taka Bone Rate** (Tiger Island), *Snellius* II 4.139B, S. of Tarupa Kecil, 06°30'S 121°8'E, edge of reef flat, 30 m, (HOLOTYPE & 4 PARATYPES: RMNH 18298; 4 PARATYPES (+ one abdomen & internal tube ridge): BM(NH) 1992.66–71; 5 PARATYPES & tube material: ZMA V. Pol. 3738; 3 PARATYPES & fragmentary tube material: USNM 130983 & 130984).

Fig. 23 *Spiraserpula sumbensis* sp. nov. A–M, Holotype. O–U, Paratype. A–D, O, Tubes showing granular overlay and faint transverse growth ridges; A, An erect part; B, also showing body, operculum & radioles *in situ*; C & D, two views of same tube fragment showing wedge-shaped dorsal and ventral ridges, both unserrated. E, Operculum. F & G, Holotype. F, Radioles showing zygomorph operculum on left, rudimentary operculum on right. G, Worm showing extent of thoracic membranes. H–K, Bayonet collar chaetae. L, Thoracic uncini. M, Anterior abdominal uncini. N, Bundle of anterior abdominal flat trumpet chaetae. O, Tube of paratype, also showing worm with its two opercula *in situ*. P, Radioles with two well-developed opercula. Q, Two views of thorax showing extent of thoracic membranes. R–U, Bayonet collar chaetae.



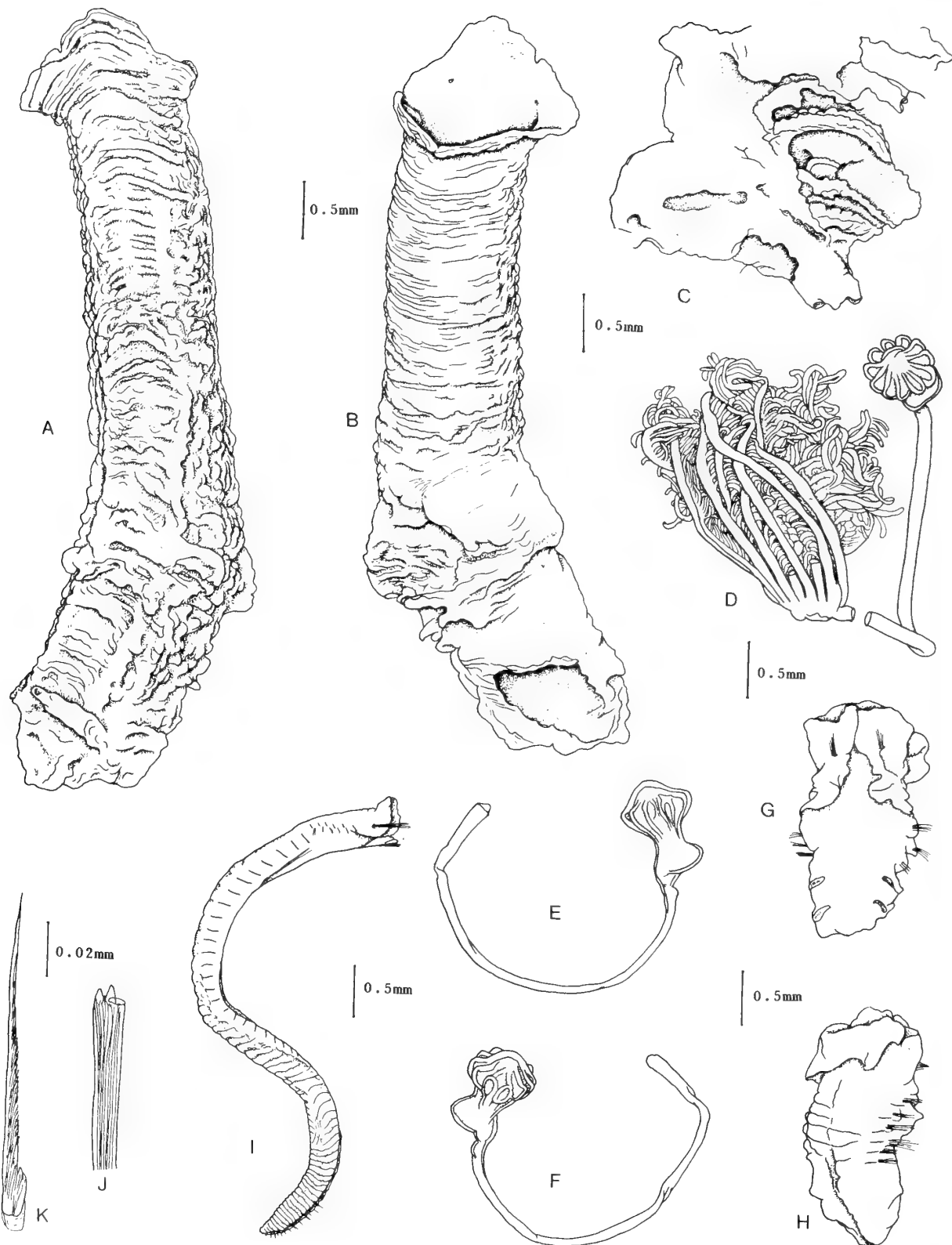


Fig. 24 *Spiraserpula iugoconvexa* sp. nov. A-K, Paratypes. A, Dorsal view of erect tube part showing longitudinal external ridges, granular overlay, transverse ridges, triangular dorsal lobe of its aperture, and an unidentified transverse epibiont at its base. B, Ventral view of same tube showing the two small ventral lobes of the aperture, rounded ventral side and fine transverse growth ridges. C, Posterior coil of tube showing a damaged dorsal ridge. D, Radioles and operculum of the right side. E & F, Same operculum showing its zygomorphy and convex distal end. G & H, Dorsal and ventral views of thorax showing the collar and extent of the thoracic membranes. I, Juvenile paratype. J, Bayonet collar chaeta, lacking blade, but showing two teeth on the basal boss. K, Newly formed chaeta from within the fascicle.

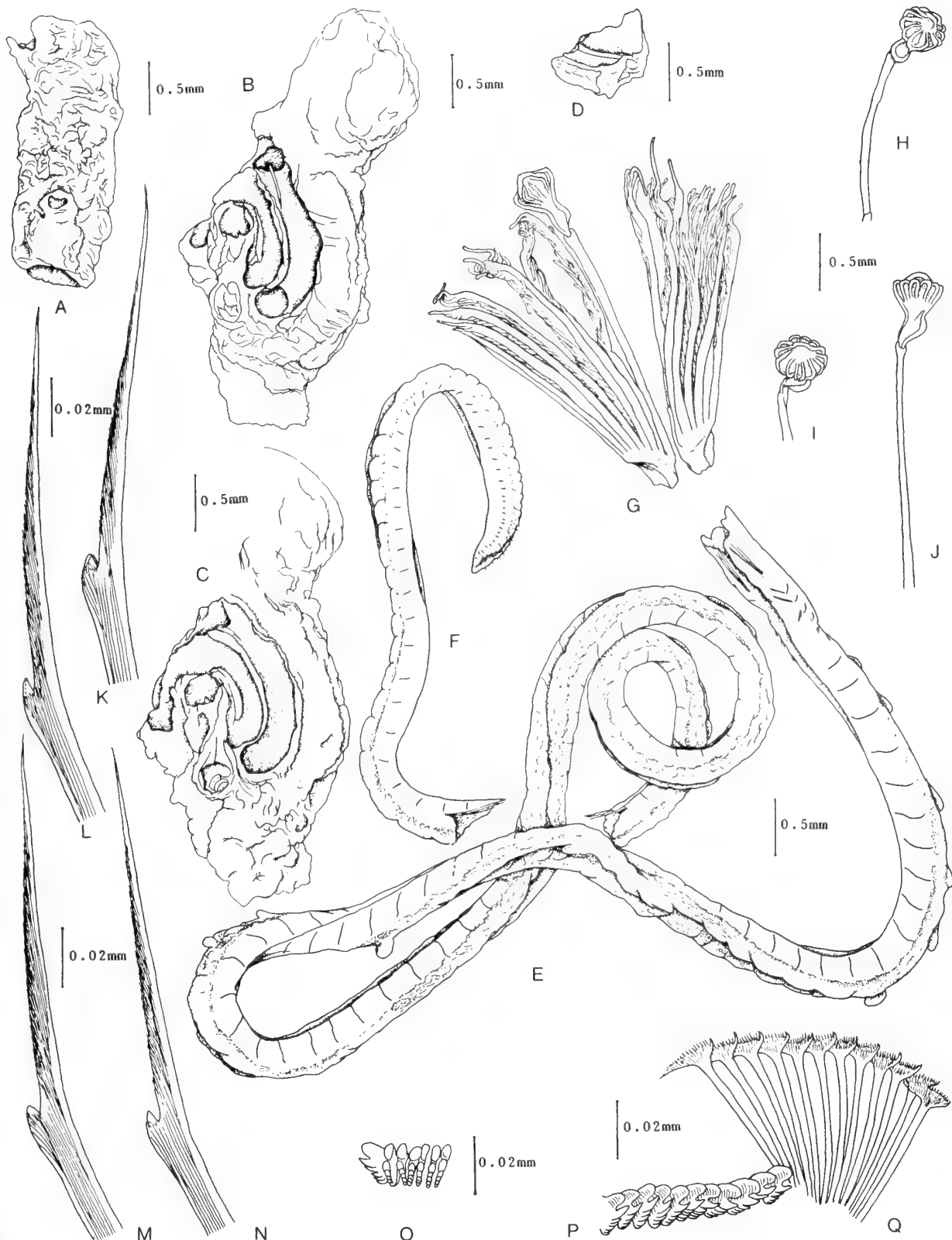


Fig. 25 *Spiraserpula iugoconvexa* sp. nov. Holotype. A, Tube fragment showing irregular surface and peculiar structure with a semilunar opening (? *Protulophila*). B & C, Views of the opened tube showing the unserrated dorsal ridge, with a somewhat flattened ridge (C, bottom left). D, Tube fragment showing ventral ridge. E-G, Entire holotype, in three parts. E & F, Body showing the dorsal longitudinal groove, the apparently glandular ventral side of the abdomen and its peculiar outpouchings. G, Radioles with operculum on the left and rudimentary operculum on the right. G-J, Four views of the zygomorph operculum with convex distal end. K-N, Bayonet collar chaetae with long slender blade, short unserrated notch and two teeth (seemingly one tooth) on the basal boss. O, Thoracic uncini. P, Anterior abdominal uncini. Q, Bundle of anterior abdominal flat trumpet chaetae.

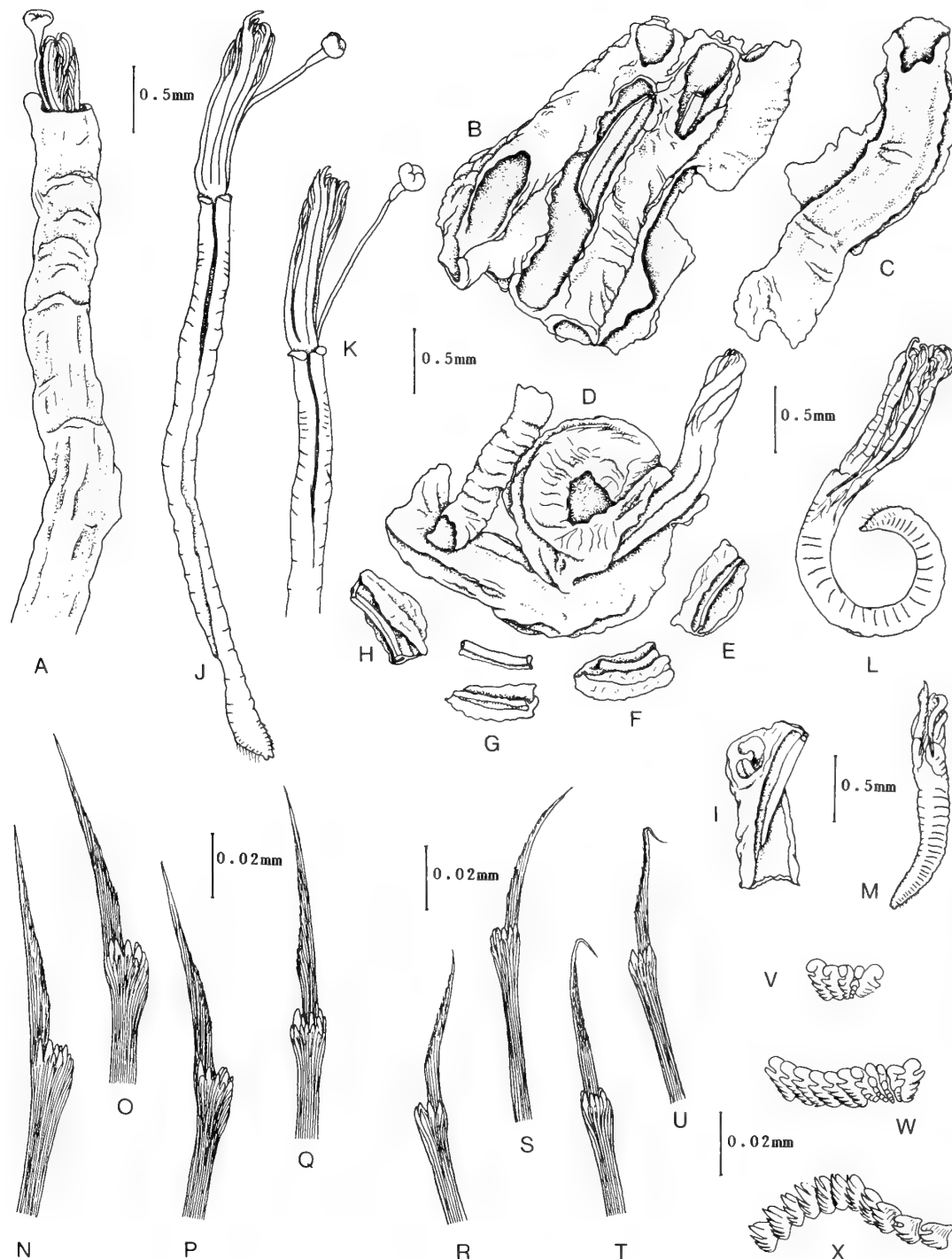


Fig. 26 *Spiraserpula snellii* sp. nov. A, J-K, N-Q, V-W, Holotype. B-L, R-U, Paratypes. M, Juvenile. A & C, Tubes showing longitudinal pigment bands, transverse bands and thickenings (A). B, Tube fragment showing unserrated ventral ridge. E-H, tube fragments in their relative positions to the unopened tube (D) showing the unserrated ventral ridge which is thickened towards the middle of the tube (G,H). I, Tube fragment showing T-shaped ventral ridge. J-K, Holotype, showing operculum, radioles, and dorsal longitudinal groove along its body. L, Paratype, juvenile without operculum. M, Smaller juvenile worm, also without operculum. N-U, Bayonet collar chaetae. V & W, Thoracic uncini. X, Anterior abdominal uncini.

Queensland (Australia): 2. **Lizard Island**, N of South Island, 14.4°S 145.3°E, reef front, sloping reef outside of lagoon and sandy bottom below, 10–17m, legit H. A. ten Hove, P. Hutchings and M. Reid, 5.iii.1986, Stn.20 (3 specimens, ZMA V. Pol. 3734, AM W20342). 3. **Lizard Island**, Palfrey

Island, S. of light-house; coral heads on sandy bottom, 7 m, legit H. A. ten Hove, 2.iii.1986, Stn.17 (1 specimen in four fragments, BM(NH) 1992.65). 4. **Lizard Island**, S. South Island; sloping silty reef, little coral cover, legit H. A. ten Hove *et al*, Stn.21, 6.iii.1986 (8+ specimens, ZMA V. Pol.

3830, BM(NH) 1993.17, AM W21677). 5. **Boulton Reef**, on scleractinian coral (*Thecopsammia regularis* Gardiner 1899), USNM 78572, dry material, legit J. C. Lang, 31.vii.1973. H. Zibrowius, who identified this, kindly drew our attention to its serpulid epifauna.

Loyalty Islands, E. of New Caledonia: 6. SW Pacific Lagoon of Beutemps-Beaupré Atoll; overhang 8 m, on heavily encrusted dendrophylliid scleractinian coral, scuba diving, dry material; MUSORSTOM 6 cruise, legit H. Zibrowius, 17.ii.1989.

Okinawa (Japan): 7. W. side of Sesoko Island, 2–3 m, on cliffside, in caves and grooves, scuba diving, on unidentified coral, legit S. Nakamura, 10.i.1989, dry material, USNM. H. Zibrowius kindly drew our attention to the serpulid epifauna.

Sinai (Egypt): 8. Strait of Tiran, at Sharks Observatory, 20–25 m; Nos. 210–213, legit H. A. ten Hove, 8.vi.1990 (2 specimens, tubes, HUJ, ZMA V. Pol. 3886).

Elat (Israel): 9. In front of Marine Biological Laboratory, 20–25 m, coral rubble; Nos. 154, a–d, legit H. A. ten Hove, 4.vi.1990. 10. Oil port, S. pier, 6–25 m, coral rubble and pillars of pier; Nos. 181, 244, 311, 339, 340, legit H. A. ten Hove, 6.vi.1990 (3 specimens, several tubes, HUJ).

TYPE LOCALITY. Taka Bone Rate (Flores Sea, Indonesia).

DESCRIPTION.

TUBES: Mustard coloured, with a pair of darker longitudinal bands in places along each flank, joined by transverse bands, especially just anterior to the thickenings found at intervals (Fig.26, A,C). They may be coiled more or less parallel to one another in the horizontal plane, mutually bonded together or spread out on the substratum and branched in places. Their external diameter is quite small, only up to about 0.6 mm. Earlier formed portions of tubes may show narrow transverse wrinkles (Fig.26, B,D). In fresh material the colour of the tube may be more brownish, and appears to fade to mustard after a few months in alcohol.

ITS consist of an unserrated ventral ridge only (Fig.26, B,E–I), which is T-shaped in cross-section towards its middle (Figs.26,G,I; 3, F), and becomes progressively less thickened both anteriorly and posteriorly (Fig.26, E,I).

WORMS: The total length of the worms ranges from 2.2 mm in the case of a juvenile, to a little more than 12.3 mm in an older individual which lacks its radioles. The complete holotype (Fig.26, J) is only 5.8 mm long. The thoracic width in all the specimens is around 0.3 mm.

An operculum may or may not be present. Younger specimens have radioles but lack opercula (Fig.26, L,M); apparently opercula appear only in older worms (Fig.26, A,J,K). The length of the operculum and peduncle in the holotype is 1.5 mm, the operculum 0.3 mm long and its diameter 0.2 mm. Its distal part is nearly globular (Fig.26,A,J,K) and, unlike the opercula of the other known members of the group, its margin is not divided into lobes, but shows about four pseudo-lobes, apparently caused by contraction in alcohol. Its proximal part is shaped like a narrow funnel, separated by a sharp constriction from the slender peduncle. A short filamentous rudimentary operculum was observed in one specimen only. It appears likely that, like the operculum, they are developed in older worms. Pinnule-free tips of radioles short. Thoracic glands were not found. Some counts and meristic data are given in Table 20:

The abdominal length in eight specimens ranged between 11.2 and 1.0 mm, and the number of segments between 48

Table 20 *S. snellii* sp. nov. Some meristic and other data of type series.

No. of specimens (n=6)	3	3			
No. of radioles	5/5	4/4			
No. of specimens (n=8)	2	1	2	2	1
No. of thoracic chaetal tufts	8/7	8/6	7/7	7/6	7/5
No. of specimens (n=3)	1	1	1		
Thoracic membrane ends	4/4	4/3	3/3		

and 22, respectively, with capillaries on the last 6 or 7.

Collar fascicles of older specimens bear about four fully formed bayonet chaetae and a developing one deep within. Each bayonet chaeta possesses a long serrated blade, a moderately long unserrated notch (1/3–1/4 the length of the entire blade), and several teeth on the basal boss (Fig.26, N–U; Pl.5, F). Thoracic uncini (Fig.26, V,W) and anterior abdominal uncini (Fig.26, X; Pl.5, G) bear 4–6 and 4–5 teeth, respectively, in a single row. Flat trumpet-shaped chaetae are typical (Pl.5, H).

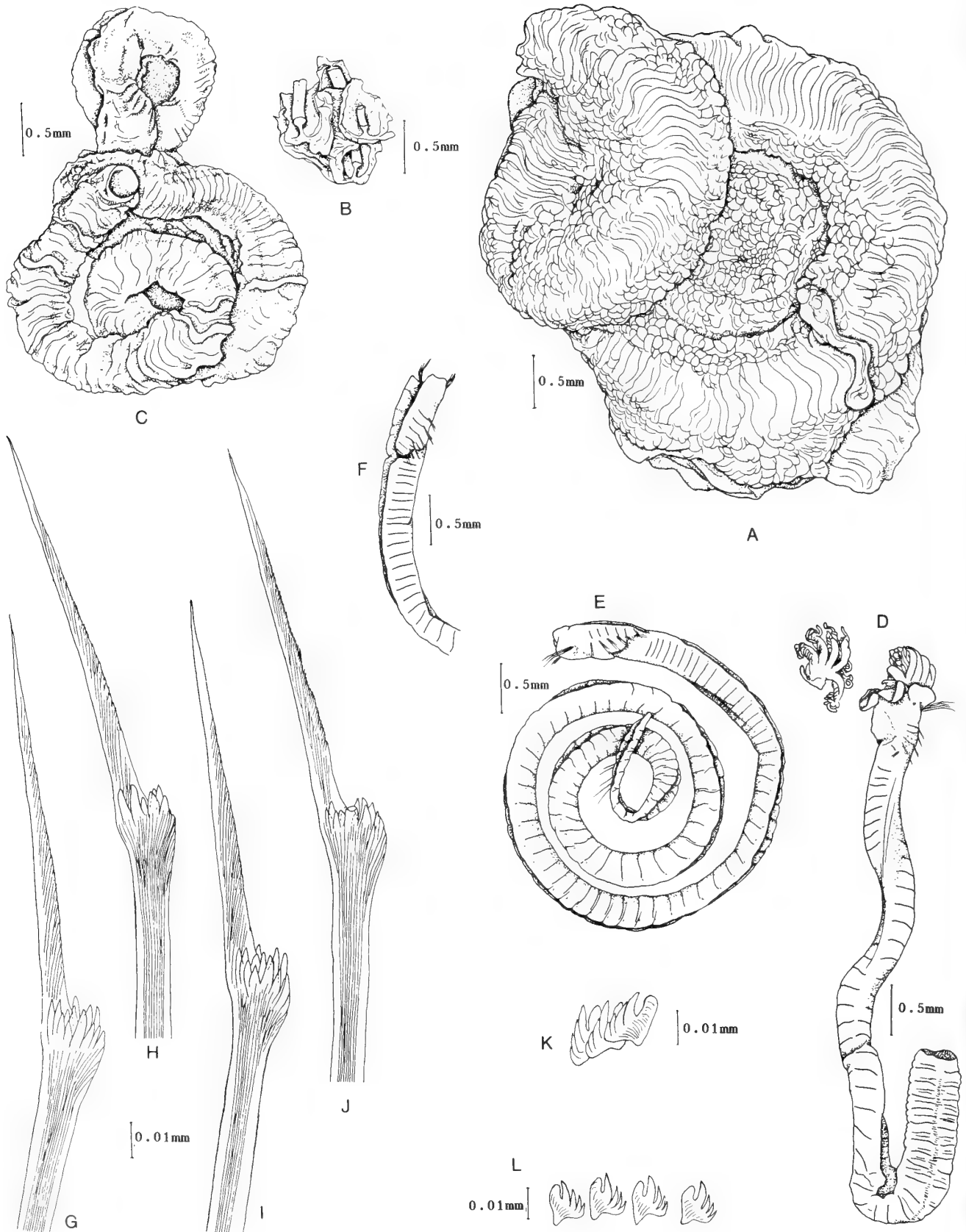
REMARKS. One single tube revealed 2 specimens: a parent with schizont closely appressed to its posterior end. Posteriorly, the abdomen of the parent was abruptly tapering (dorso-ventrally), with long capillaries. Lying between those, the three pairs of radioles of the schizont could be found. It had a narrow, still not fully developed thorax with 7/6 chaetal tufts, followed by a well-formed abdomen with 17 chaetigers (the last 7 with capillaries). The entire schizont was folded over the ventral internal ridge.

COLLECTIONS FROM OTHER LOCALITIES. The specimens in sample 2 from Queensland agree with those in the Indonesian sample with regard to the overall mustard colour. Against this background colouration there are darker mustard to brown longitudinal bands, which are variable. One of the three available tubes has a pair of lateral longitudinal bands, lacking in places. The second tube has a thin median longitudinal stripe in addition. The third has a pair of mustard yellow longitudinal bands laterally, and a broad brownish median band which is partially divided into two bands by a narrow, yellow longitudinal band.

They are coiled upon themselves either individually or mutually bonded together. The coils are more or less concentric, low, flattened against the substratum, and bonded together (Fig.27, A). The maximum external tube diameter is 1.2 mm. The granular overlay consists of a median longitudinal band made up of broad, transverse, forwardly-directed scutes, and a narrow band of smaller granules laterally (Fig.27, A). At irregular intervals there are wavy, thickened, peristome-shaped transverse ridges.

ITS agree with those of the Indonesian specimens. They consist of only an unserrated ventral ridge. Its edge is smooth and, in cross-sectional appearance, varies from being wedge-shaped to thickened and T-shaped at its maximal development (Fig.27, B). The cross-bar of the T may also be curved outwards and bear a shallow longitudinal depression. The mid-ventral longitudinal abdominal groove is applied to this ridge.

Three worms were removed from the tubes. One has a damaged thorax and an incomplete abdomen, while the second lacks the radioles of both sides, the third is broken in 4 fragments. The former (Fig.27,D), is 0.4 mm wide in the



thorax, and has 6 radioles and a short club-shaped rudimentary operculum on each side. The radioles are about 0.4 mm long and end in short pinnule-free tips. Two clusters of dark brown prostomial ocelli are present. There are 7 thoracic chaetal tufts on one side, but the number on the other side and the extent of the thoracic membranes cannot be determined due to the damaged thorax.

The first worm is spirally coiled along the substratal plane (Fig. 27, E). The length of the thorax and abdomen is 13.8 mm, of which the posterior portion of about 1.18 mm is abruptly narrower than the rest of the abdomen. The entire length of the third worm is about 7.0 mm, radioles 1.3 mm, thorax and abdomen 5.7 mm; it has 7/6 radioles, and thoracic width of 0.35 mm.

There are 7 thoracic chaetal tufts on each side in one worm, 6/7 in the other. The thoracic membranes end between chaetal tufts 6 and 7 on the left, and 5 and 6 on the right (Fig. 27, E, F). Thoracic glands are absent. The number of abdominal segments is 102, with capillaries on the last 6. A mid-ventral longitudinal groove traverses the entire abdomen and thorax (Fig. 27, E, F).

Each collar fascicle bears about 4 bayonet chaetae. They have long serrated blades, a short unserrated notch, and several teeth on the basal boss (Fig. 27, G–J). Thoracic uncini usually bear 4 teeth in a single row (Fig. 27, K). The anterior abdominal uncini also possess 4 teeth in a single row, but the 3 posterior teeth are not closely appressed, as in the Indonesian specimens (Fig. 27, L). Flat trumpet chaetae number about 3 per bundle. Since their edge is curved, details on the anterior tooth cannot be observed.

The third sample from Lizard Island, Queensland agrees with the first and the Indonesian specimens in all important characters (Fig. 27, A–J). The fully formed operculum is an unlobed funnel with a shallow distal concavity (Fig. 28, C, D), while in the earlier stages it is spherical or nearly spherical (Fig. 28, E–G).

The dry tubes from Loyalty Islands (Fig. 28, K–Q) appeared to be brownish, but regained the typical mustard colouration when immersed in alcohol. One fragment shows branching (Fig. 28, K). Internally there is only a smooth ventral ridge (Fig. 28, N–Q), which is clearly T-shaped in places (Fig. 28, Q); it is markedly so and occupies a larger part of the lumen in some tubes which are comparatively very thick-walled (Fig. 28, N).

The collection from Ras Mohammed, Sinai, consists of tubes with fragments of worms (Fig. 28, R–V). The tubes have an overall mustard colour, but the anterior portions (Fig. 28, R, S) have pinkish peristomes, and a conspicuous granular overlay along the lateral borders of the attached portions (Fig. 28, S). The medial overlay is scute-shaped, but not as prominent as in the first Lizard Island sample. A smooth ventral ridge is present (Fig. 28, T–W), which is T-shaped in its fully formed condition (Fig. 28, T, U, W). Those details of the worm that still could be observed (collar chaetae, ends of thoracic membranes) agree with the data given above.

The samples from Elat, Israel, agree with regard to tube

colouration, the smooth ventral longitudinal ridge and other important characters. No. 154 is a single specimen on a piece of coral rubble. The granular overlay is translucent in places; transverse scutes are not seen medially, but this may be because it is a juvenile. The worm has a total length of 3.6 mm; reddish prostomial ocellar clusters are present; its thorax is 0.2 mm wide; gills 1.0 mm long, with short pinnule-free tips; the number of thoracic chaetal tufts L?/R7; its abdomen 1.9 mm long, with 24 segments and capillaries on the last 4. There are 3 bayonet chaetae per fascicle, each with an elongated blade, a short unserrated notch and several teeth on the basal boss. Anterior abdominal uncini bear 4 teeth in a single row. An operculum had yet to be developed. However, an operculum was observed in sample 311. A schizont was separated from sample 244.

ETYMOLOGY. Named after the Indonesian-Dutch Snellius II Expedition which enabled the second author to collect extensively in Indonesian waters.

HABITAT AND DISTRIBUTION. A reef dweller occurring at depths of about 15–30 m. Appears to be the most widely distributed species of the genus. Hitherto collected from the northern Red Sea, Indonesia (Flores Sea), Australia (Great Barrier Reef) and W. Pacific (S. Japan to New Caledonia).

Spiraserpula lineatuba (Straughan, 1967)

(Figs. 29, A–O; 30, A–M; 3, L; Pl. 1, A, C & D, Pl. 3, E–G)

SYNONYMY. *Serpula lineatuba* Straughan, 1967, pp. 211–212, Fig. 5a–g.

MATERIAL EXAMINED.

New South Wales: 1. Sydney, Long Reef, underside of rocks, LWS, 27.ii.1965, legit D. Straughan (HOLOTYPE, AM4018). 2. Sydney, Long Reef, rocks just below LWS, Colloroy, Stn. 30, 27.i.1964 (Topotypical material, 2 specimens and several tubes, AM4019, ZMA V. Pol. 3450, BM(NH) 1992.51). 3. Norah Head, at foot of light house, from bottom of tidal pools at low-tide, from undersides of boulders, legit H. A. ten Hove, 12.iv.1986, Stn. 31 (5 out of several specimens, AM W20340). 4. Split Solitary Island, rocky island area with corals, algae and little sand, from ceiling of small cave, 12–19 m, legit H. A. ten Hove, P. Hutchings and R. Phipps, 26.iv.1986, Stn. 36 (18 out of several specimens, ZMA V. Pol. 3709, USNM 130996, BM(NH) 1992.40–50, AM W20163, QM, NSMT). 5. South Solitary Island, S of light house, rocky area, cobbles and corals, little sand, 12–20 m, legit H. A. ten Hove, P. Hutchings and R. Phipps, 27.iv.1986, Stn. 37 (3 out of several specimens, BM(NH) 1992.52–60).

TYPE LOCALITY. Sydney, Long Reef (Australia).

DESCRIPTION.

According to the original description (Straughan, 1967), the tube is circular in cross-section, white, with a pair of dark pink lateral longitudinal stripes, pale pink dorsal surface. The

Fig. 27 *Spiraserpula snellii* sp. nov. From Stn. 20, Lizard Island, Australia: A, Adult tube showing flattened coil form, granular overlay, which is scutate medially, granular laterally and has a transverse thickened peristome. B, Aggregation of tube fragments with unserrated ventral ridge, T-shaped in cross-section. C, Scutate juvenile tube with some transverse thickenings; granular overlay not yet developed. D, worm showing radioles, rudimentary operculum and collar. E, worm from tube figured in A, showing thoracic membrane, ventral longitudinal groove. F, Anterior part of latter, showing lack of apron and thoracic membrane ending on the 6th chaetiger on the left side. G–J, Bayonet chaetae, all from same fascicle. K, Thoracic uncini. L, Anterior abdominal uncini.

total length of the worm ranges from 4.5–6.5 mm. There are 4–6 pairs of branchiae with pinnule-free tips. A hollow operculum with about 22 lobes is present on one side, with a pseudoperculum on the other. The collar has a pair of lateral elongations on the median lobe. The thorax has 9 or 10 segments on each side, and the bayonet collar chaetae have 2 conical processes at the base of the blade.

The holotype (AM W4018) is in very poor condition. When it was examined by the second author in 1979, the poorly preserved worm, still within its tube, lacked both an operculum and a rudimentary operculum, although there appeared to have been one on one side and none on the other. Other observations were as follows: A cluster of pigmented ocelli present at the base of each branchial lobe; bayonet collar chaetae possess 2 conical teeth, with 1–3 accessory conical teeth; the anterior abdominal uncini of two types: some with a single row of teeth, others in which the posterior tooth is split into two; middle abdominal uncini appeared to possess 7 simple teeth in side view; in edge view, however, four anterior teeth are single and the rest are rows of 3 minute teeth each.

However, examination of topotypical material collected on the same date as the holotype and determined by Straughan (AM 4019, ZMA V.Pol. 3450) yielded the following additional data: The tube has a pair of light pink longitudinal bands (Fig. 29, A), not clearly defined dark pink stripes as mentioned and figured in the original description. It is coiled, somewhat flattened against the substratum, but the free surface is rounded. The coils are bonded together. A granular overlay is present, but it is extremely fine and can only be seen in places, under special illumination (Fig. 29, F). A short erect portion is present (Fig. 29, A,B), with a four-lobed peristome similar to that of *S. massiliensis*.

The most important data obtained during the present study of this topotypical material is that *S. lineatuba* has ITS. They consist of an unserrated dorsal ridge along the convex wall (Fig. 29, B,C,E,F), and a serrated ventral ridge along the opposite wall (Figs. 29, D,F; 3, L). The former may be high in the first formed coil (Fig. 29, E, F, bottom left), or low anteriorly (Fig. 29, B,C), and is wedge-, tongue- to somewhat T-shaped in cross-section.

The worm is 6.5 mm long, its thorax is 0.5 mm wide, and its abdomen is 4.5 mm long. There are 5 radioles and a slender rudimentary operculum on one side. The median lobe of the collar has only one forwardly directed process, in contrast with the original description, indicating that this is a variable feature. There are 7 pairs of thoracic chaetal tufts, and the abdomen has 49 segments, with capillaries on the last 19. Two clusters of prostomial ocelli are present and the thoracic membranes do not extend to the last thoracic chaetigers, but end on the fourth and fifth.

There are 5 bayonet chaetae in each collar fascicle, each with a moderately long serrated blade, a moderately long unserrated notch which is 1/3–1/4 the length of the blade, and 2 or 3 conical teeth on the basal boss (Fig. 29, G–J; Pl. 3, E). In bayonets with two large teeth, a single accessory tooth may

be present between them (Fig. 29, G,H,J). Thoracic uncini bear 5 or 6 teeth. As seen in edge view, in the outermost uncini of the row, 3 to 5 of the anterior teeth are single, while the remaining teeth are subdivided into 2 or more smaller teeth which form a short, rasp-shaped posterior cluster (Fig. 29, L). Anterior abdominal uncini are similar (Fig. 29, N). However, SEM of anterior abdominal uncini of another specimen showed a single row of teeth in edge view (Pl. 3, F). It appears, therefore, that both types of uncini may sometimes be present. Posterior abdominal uncini are rasp-shaped, except for the single anterior tooth. The uncini of the intermediate region show a transition between the two types. Flat trumpet chaetae number about 5–7 per fascicle (Fig. 29, N; Pl. 3, G).

A more complete account of the species, however, was obtained from numerous well-preserved specimens collected in 1986 from Split Solitary Island.

TUBES: Have the colouration described above, including the pair of light to somewhat darker pink lateral longitudinal bands. They occur in aggregations of a few to numerous individuals, highly coiled amongst themselves and mutually bonded together, particularly at their bases (Fig. 29, O). Erect parts are sometimes present, and they may bear four-lobed peristomes (Fig. 30, A). The uncoiled part of one of the longest tubes measures 26.7 mm; together with its coiled part it is approximately 30.0 mm long, and its maximum external width is 1.1 mm.

ITS consist of an unserrated dorsal ridge, a serrated ventral ridge and, usually, a pair of accessory dorso-lateral ridges (Figs. 29, O, middle left; 30, B,C; 3, L; Pl. 1, A,C,D). The dorsal and ventral ridges of the tube are applied to corresponding longitudinal mid-dorsal and mid-ventral abdominal grooves (Figs. 30, D–F).

Eighteen worms from Split Solitary Island provided important additional data. Measurements and other meristic data from 8 complete specimens of total lengths ranging between 15.9 mm and 1.3 mm presented in Table 21 show that the worms can attain two and a half times the length mentioned in the original description. The maximum number of abdominal segments counted is 89:

Thirteen complete anterior ends all possess an operculum on one side, a rudimentary operculum on the other, and 5 pairs of radioles. The pinnule-free tips are about 1/4 the length of the radioles and are as thick as the pinnules (Fig. 30, D,E). The length of the operculum together with its peduncle ranges between 0.8 mm in the smallest specimen to 1.6 mm in the largest; the length of the operculum itself from 0.3 mm to 0.7 mm, and its diameter from 0.4 mm to 0.6 mm, respectively. All the opercula are zygomorph (Fig. 30, D,F), their distal ends are concave and the radii end in somewhat pointed lobes. Many of the latter are actually double, the sub-dividing grooves being only about 1/3 the length of the main interradial grooves which extend to about half the opercular length. Thus the total number of about 17–23 radii end in about double the number of marginal lobes (Fig. 30, D–F). The constriction between the peduncle and the operculum is

Fig. 28 *Spiraserpula snellii* sp. nov. A–J, from Stn. 21, Lizard Island, Australia. K–Q, From Loyalty Is. R–W, from Egypt. A–B, Tube lacking scutes and granular overlay, but with faint transverse grooves between transverse areas (representing scutes?). D–E, Same worm with fully formed operculum. E–G, worms showing early vesicular operculum. H, Bayonet chaetae. I, Thoracic uncini. J, Anterior abdominal uncini. K, Anterior fragment of a tube showing branching and a peristome. L, Another fragment showing transverse ridges. M, Juvenile tube. N, Fractured end of a tube showing a thick wall and a T-shaped ventral ridge occupying most of its lumen. O–Q, Tube fragments with varying form and thickness of the T-shaped ventral ridge. R & S, Anterior tube fragments, R with peristomes. T–W, tube aggregations with fractured ends showing the T-shaped ventral ridge. W, V, with longitudinal view of ventral ridge.

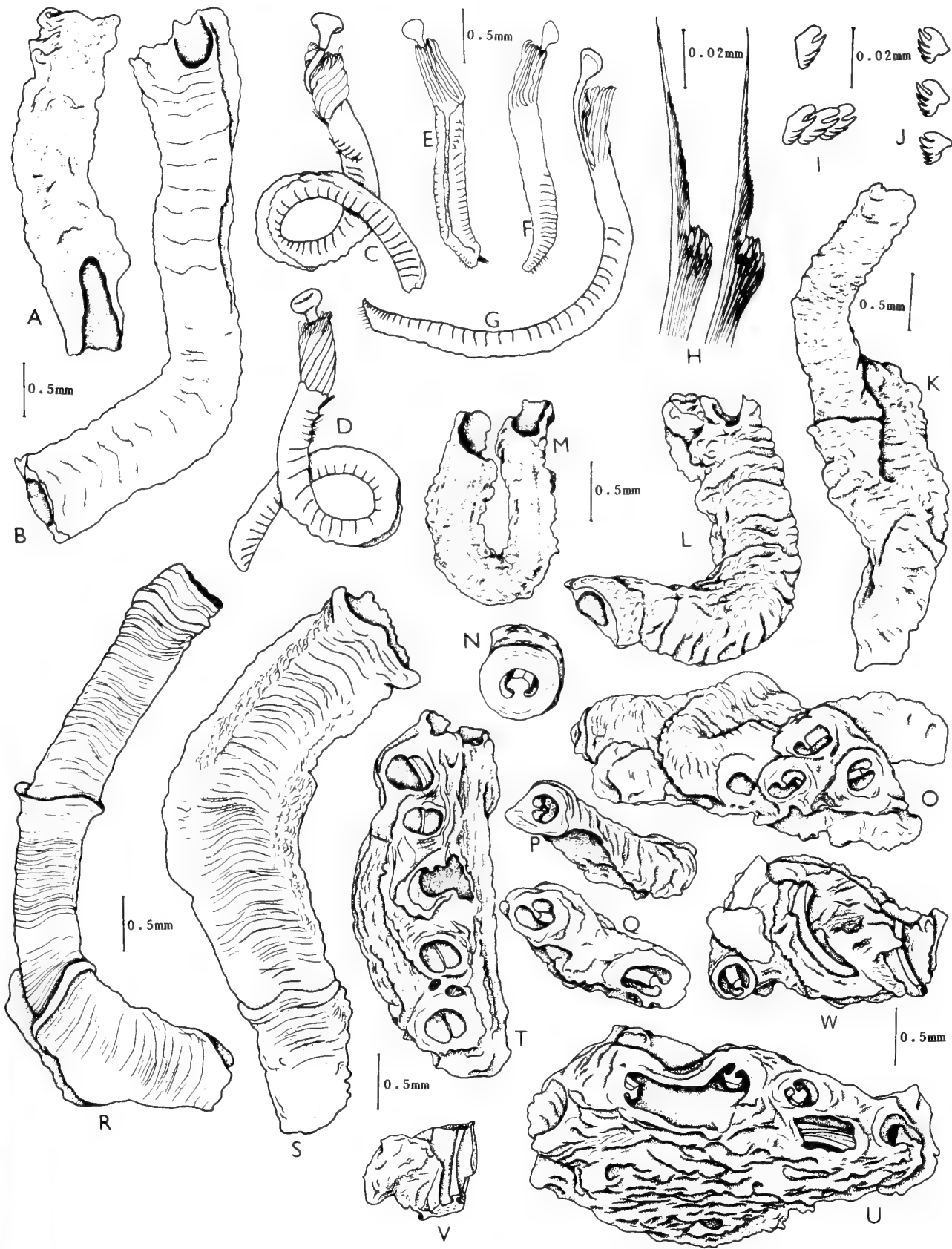


Table 21 *S. lineatuba* (Straughan). Measurements and counts from Split Solitary Island material.

Specimen no.	Total length	Width of thorax (mm)	Length of abdomen (mm)	No. of abdominal segments	Capillaries on
1	15.9	0.6	13.2	89	13
2	15.7	0.6	12.6	85	13
3	15.7	0.5	12.7	81	12
4	13.9	0.5	10.9	58	17
5	13.0	0.5	12.7	81	13
6	10.1	0.5	10.9	58	17
7	9.3	0.5	6.8	78	16
8	1.3	0.5	0.4	45	25

Table 22 *S. lineatuba* (Straughan). Number of thoracic chaetal tufts and extent of the thoracic membranes in specimens from Split Solitary Island.

No. of specimens (18)	1	1	4	4	1	4	2	1
No. of thor. chaetal tufts	10/10	10/9	10/8	9/9	9/8	8/8	8/7	7/7
No. of specimens (15)	1	1	1	4	1	1	2	1
Thoracic membr. ends	7/5	6/4	5/5	5/4	5/3	4/4	4/3	4/2
							3/3	3/2

sharp, and the diameter of the distal end of the former varies from 1/3 to 2/3 that of the base of the latter.

The median lobe of the collar shows one or more anteriorly directed processes in some specimens, none in others. Up to 8 bayonet chaetae have been counted in a collar fascicle. A pair of ventral thoracic glands is present (Fig.30, E). The number of thoracic chaetal tufts on each side varies from 7–10, and the thoracic membranes end on the 3rd to 6th chaetigers, as shown in Table 22.

The specimens from South Solitary Island and Norah Head agree with the above description.

LIVE MATERIAL. No records.

HABITAT AND DISTRIBUTION. The species occurs from the tidal zone down to about 20 m. It was very abundant on a ceiling of a small cave at a depth of 12–19 m, forming aggregations of up to 35 mm thick, and superficially resembles *S. ypsilon* from a similar habitat in the Cape Verde Islands. It has hitherto been collected only from N.S.W.

***Spiraserpula discifera* sp. nov.**
(Figs.31, A–M; 3, M)

MATERIAL EXAMINED.

New South Wales: Sydney, Long Reef, from undersides of rocks in and bottom of tidal pools, mats of *Serpula rubens*

Straughan, 29.iii.1986, legit H. A. ten Hove and P. Hutchings, Stn. 30 (HOLOTYPE, AM W20390).

TYPE LOCALITY. Sydney, Long Reef (Australia).

DESCRIPTION.

TUBE: Pink, with whitish lateral attachment areas and very fine transverse wrinkles. The median tube parts are of a paler pink colour than the medio-lateral parts, in fresh material. A fine granular overlay is present, which can be seen at certain angles of illumination. The lateral borders of the tube are glassy and transparent. Irregularly laid along the outer surface of the tube, and more or less perpendicular to it, are small semilunar to crescentic discs (Fig.31, A–C,E). They are very thin, pink, glassy and transparent, and their axes are at various angles to the longitudinal axis of the tube. Some of them are even attached to the substratum just outside the tube (Fig.31, B). The maximum external diameter of the tube is 0.85 mm.

ITS consist of a serrated ventral ridge along its concave wall (Fig.31, E), and a smooth dorsal ridge. In addition, pink disks are found on the inside too, on either side of the serrated ventral ridge (Figs.31, D; 3, M). In some cases the discs appear to be through and through the wall. The mid-ventral longitudinal groove of the abdomen (Fig.31, F) is applied to the serrated ventral ridge. The worm appears to have a remarkable ability to adjust its abdominal segments in relation to these sharp discs within the tube.

WORM: Although only one specimen is available, it is complete (Fig.31, F). Its total length is 7.7 mm, thoracic width 0.56 mm; the abdomen is 6.6 mm long and has about 56 segments, the last 20 with capillaries. There are 6 radioles and a rudimentary operculum on each side. A cluster of blackish prostomial ocelli is present at the base of the radioles on each side. There are 8 pairs of thoracic chaetal tufts. Where the thoracic membranes of the two sides end precisely is not clear since the thorax is highly contracted (Fig.31, F,G), but an apron is absent. No thoracic glands were discernible.

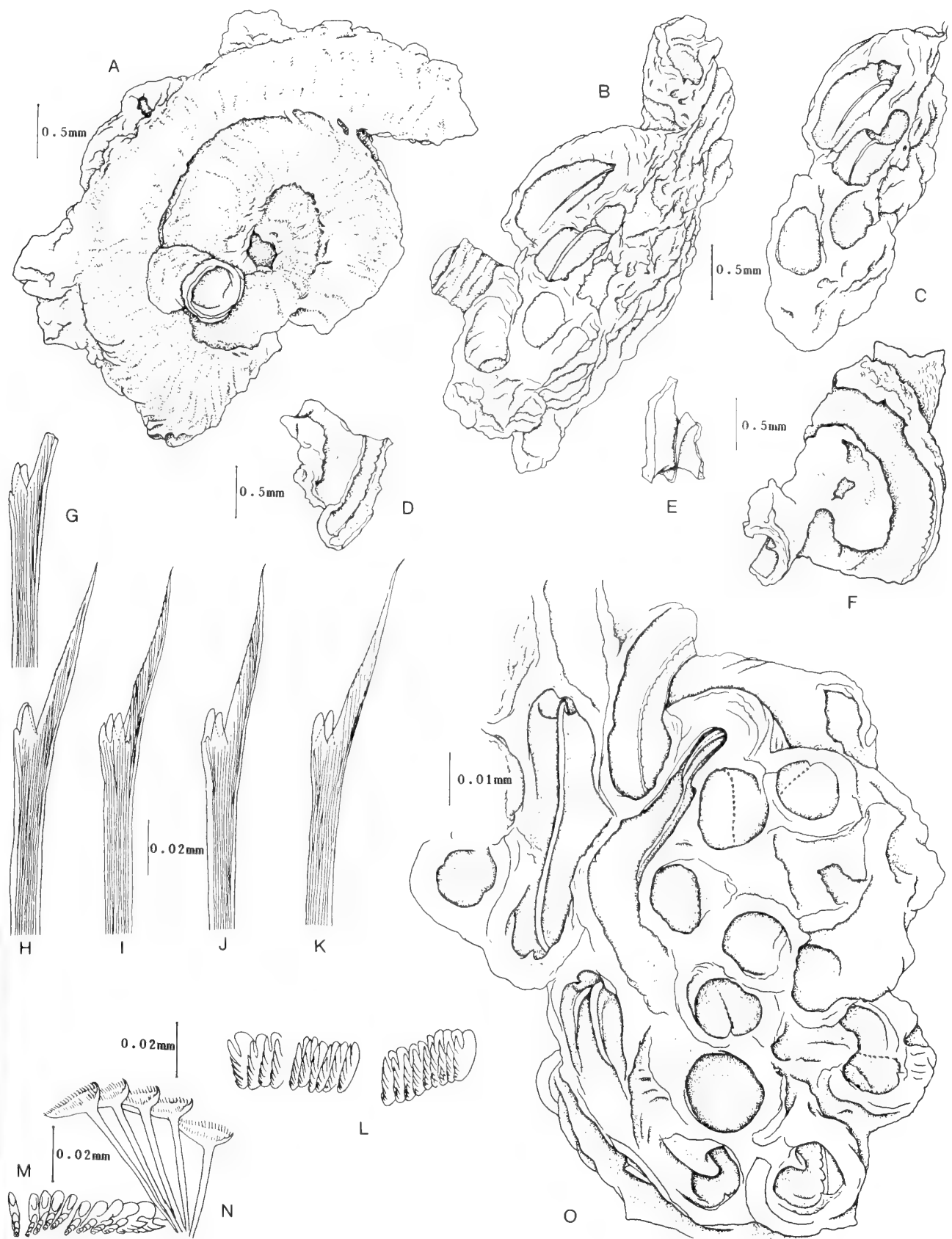
The number of bayonet chaetae, 6 in each collar fascicle, is high in relation to the size of the worm. Their serrated blades are moderately long, the unserrated notch is about 1/3 the length of the blade, and there are only 2–4 teeth on the basal boss (Fig.31,H–M). A few small accessory teeth may be present. Thoracic and anterior abdominal uncini bear about 6 and 5 teeth, respectively, in a single row.

ETYMOLOGY. diskos (Gr.) = discus; pherein (Gr.) = to carry.

LIVE MATERIAL. Animal is orange in colour, with transparent branchiae.

HABITAT AND DISTRIBUTION. *S. discifera* occurs intertidally on rocks. It has hitherto been collected only from Sydney.

Fig. 29 *Spiraserpula lineatuba* (Straughan, 1967). A–N, From topotypical material, Straughan's original collection, NSW, Long Reef, AM4019, ZMA V. Pol. 3450. O, From NSW, Split Solitary Island. A & B, Two views of same coiled tube with an erect part ending in peristome, with longitudinal colour bands in A. B & C, Same tube with posterior coils opened to show the dorsal ridge. D & F, Tube fragments with serrated ventral ridge. E, Posterior tube fragment with unserrated dorsal ridge. G–K, Bayonet collar chaetae. L, Thoracic uncini with more than one row of teeth posteriorly. M, Anterior abdominal uncini. N, Bundle of flat trumpet chaetae from same abdominal segment. O, Aggregation of tubes showing serrated ventral ridges along concave walls, unserrated dorsal ridges along convex walls, and accessory dorso-lateral ridges (bottom left).



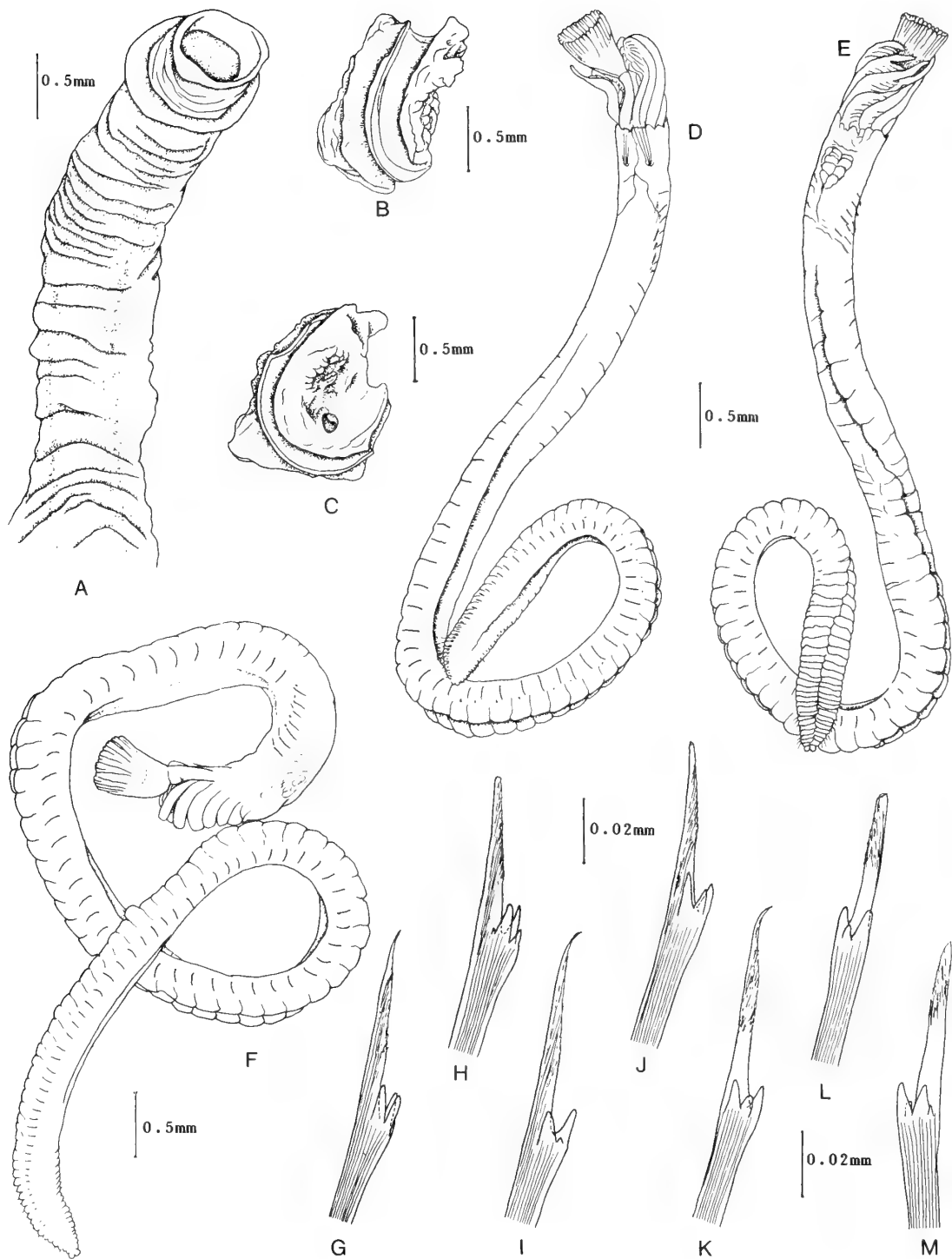


Fig. 30 *Spiraserpula lineatuba* (Straughan, 1967). A–M, From NSW, Split Solitary Island. A, Erect tube part showing fine transverse wrinkles and longitudinal colour bands. B & C, Views of same posterior coil, opened, exposing unserrated dorsal ridge. D & E, Two views of the same worm, and F, another worm, showing zygomorph operculum, extent of thoracic membranes, and dorsal and ventral abdominal grooves. G–M, Bayonet chaetae showing variations in the teeth on the basal boss.

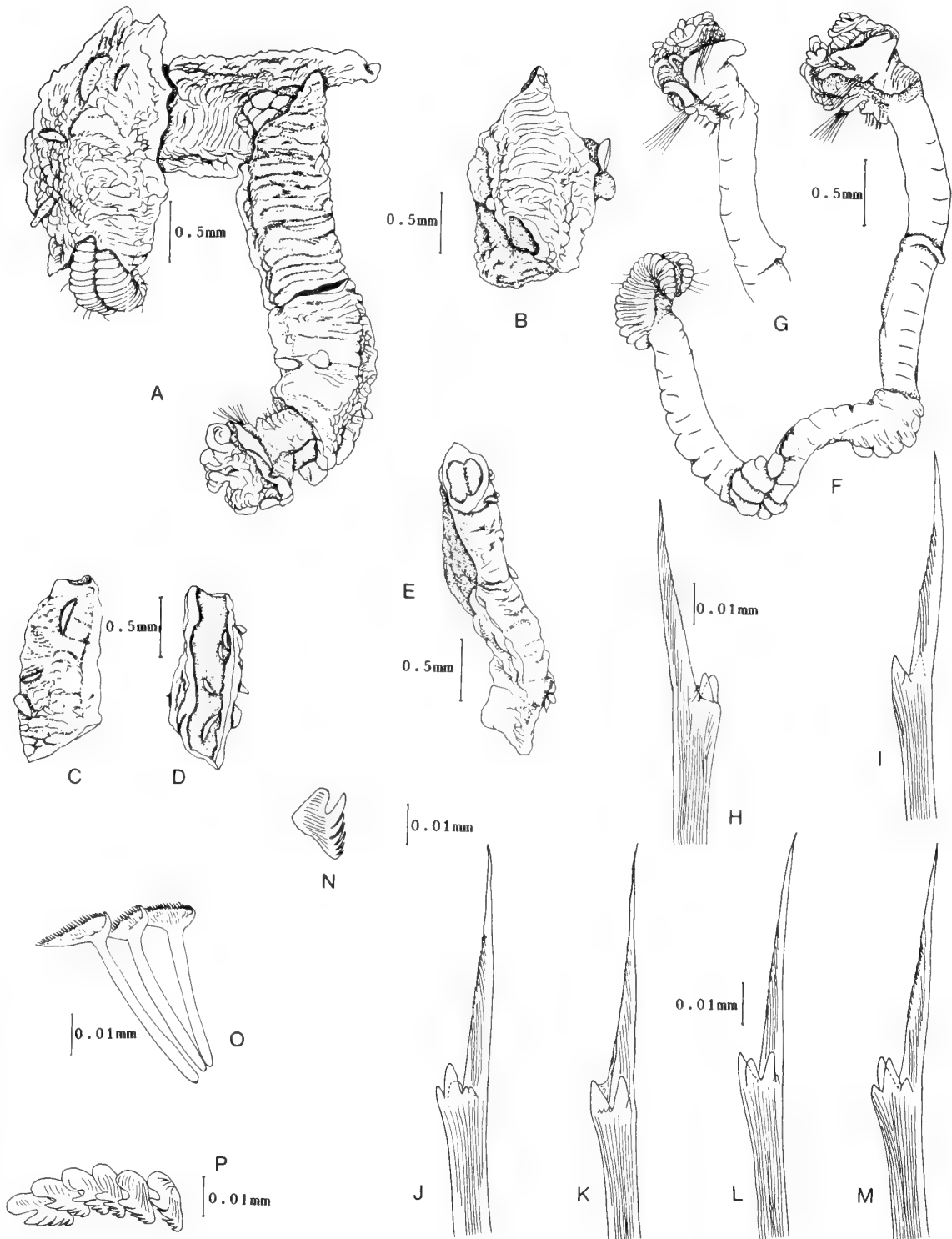


Fig. 31 *Spiraserpula discifera* sp. nov. From holotype. A, Fractured tube showing transverse wrinkles, granular overlay, and characteristic sharp crescentic discs on outer surface. B, Tube fragment, with one of the discs fixed to the substratum, adjacent to the tube. C & D, Opposite halves of tube fragment split open to show the ITS: a serrated ventral ridge (in longitudinal view), and a lateral row of transparent crescentic discs. E, Tube fragment with internal serrated ventral ridge and external crescentic discs. F, Worm, showing ventral abdominal groove. G, Anterior part of worm showing thorax, collar and thoracic membrane. H-M, Bayonet chaetae, all from same fascicle. N, Thoracic uncinus. O, Abdominal chaetae. P, Anterior abdominal uncini.

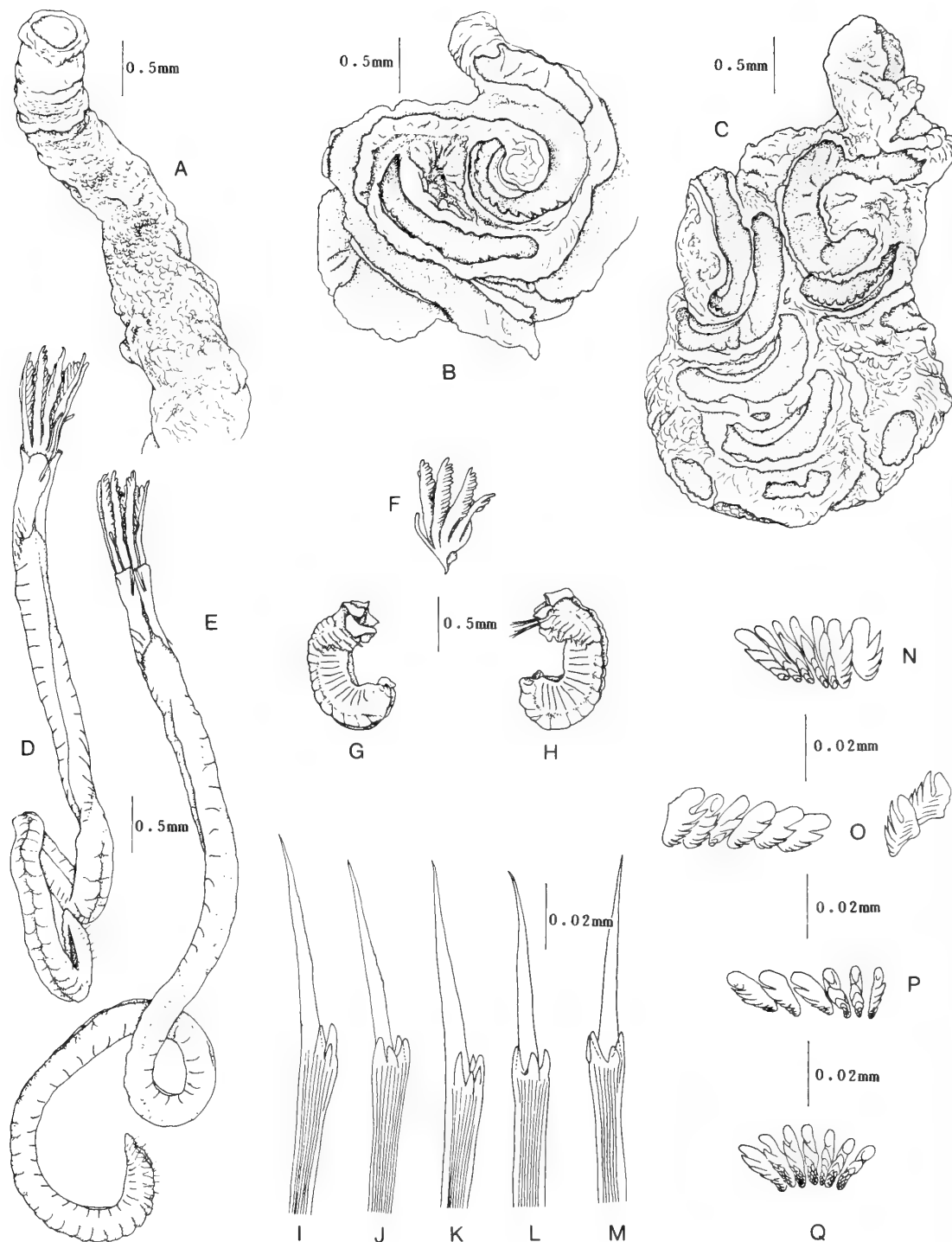


Fig. 32 *Spiraserpula minuta* (Straughan, 1967). A–Q, From Port Douglas, N. Queensland. A, Erect part of tube showing granular overlay. B & C, Substratal view of tubes opened to show ITS: an unserrated dorsal ridge along the convex wall, and a serrated ventral ridge opposite. D & E, Complete worm showing filamentous rudimentary opercula, extent of thoracic membranes and dorsal and ventral longitudinal abdominal grooves. F, Branchial crown and rudimentary operculum of right side from another worm. G, Two views of the anterior part of a worm fixed outside the tube, collar and thoracic membranes. I–M, Five bayonet chaetae from one fascicle. N, Thoracic uncini. O, Anterior abdominal uncini. P, Uncini from a torus middle abdominal region. Q, Posterior abdominal uncini.

Spiraserpula minuta (Straughan, 1967)
(Figs.32, A–Q; 3, N)

Synonymy: *Pseudoserpula minuta* Straughan, 1967, p.216, Fig.6, h–l.

MATERIAL EXAMINED.

Queensland (Australia): 1. Port Douglas, sheltered side of rocks, near LWM, legit D. Straughan, 17.i.1963 (HOLOTYPE AM W4062). 2. Same locality and date, legit D. Straughan: (25 studied out of numerous specimens, AM W4059).

TYPE LOCALITY. Port Douglas, Queensland (Australia).

DESCRIPTION. According to the original description, the tubes are white, round, and may have a pink tinge. An operculum or pseudopercula (=rudimentary opercula) are absent, there are 5 pairs of radioles, the number of thoracic chaetigers is 7 or 8, and bayonet collar chaetae have 2 or 3 blunt teeth on the basal boss (Straughan, 1967). *Vide* discussion on the taxonomy which follows this description.

The holotype (AM W4062) was examined by the second author in 1979. Upon removal of the worm from its tube, it lacked a branchial crown and its abdomen consisted of 48 segments, the last 6 with capillaries. However, the present study revealed that AM W4059, which was collected from the same locality and on the same date by Straughan, contains several well-preserved specimens, and the following description is based on 25 of them.

TUBES: Whitish in juveniles, with a very faint overall pinkish tinge in adults but, unlike *S. lineatuba* (Straughan), lacking a pair of pink longitudinal bands. They occur in aggregations of a few to several individuals which are mutually bonded at their bases (Fig.32, C). Their anterior ends are often free and erect (Fig.32, A). A very fine granular overlay is present (Fig.32, A).

ITS, located in the first formed parts of the tube, consist of an unserrated dorsal ridge, which is somewhat T-shaped in cross-section, along its convex wall, and a serrated ridge along the opposite side (Figs.32, B,C; 3, N). The posterior end of the abdomen often shows a short mid-dorsal longitudinal groove, into which the unserrated dorsal ridge of the tube fits (Fig.32, D). The serrated ventral ridge of the tube fits into a mid-ventral longitudinal groove in the abdomen (Fig.32, D).

WORMS: Out of the 25 specimens only 11 are complete. Three have total lengths of over 10 mm, three between 8.0 and 10.0 mm, and five between 6.4 and 8.0 mm. Measurements and meristic data of the longest and two smallest specimens are presented in Table 23:

Quite in contrast to the original description, nineteen specimens with complete anterior ends all possess a pair of

Table 23 *S. minuta* (Straughan). Measurements and meristic data of three specimens.

Specimen no.	Total length	Thoracic width (mm)	Length of abdomen (mm)	No. of segments	Capillaries on
1	13.7	0.5	11.3	82	11
2	7.5	0.5	5.5	48	8
3	6.5	0.5	5.2	78	10

Table 24 *S. minuta* (Straughan). Meristic and other data.

No. of specimens (n=19)	2	14	3				
No. of radioles	6/5	5/5	5/4				
No. of specimens (n=20)	1	2	8	4	2	2	1
No. of thor. chaetal tufts	9/8	9/7	8/8	8/7	8/6	7/7	7/6
No. of specimens (n=17)	2	3	5	6	1		
Thor. membranes end	6/5	6/4	5/4	4/4	4/3		

rudimentary opercula (Fig.32, D–F). A fully formed operculum is absent. The length of the radioles, ranges between 1.0 mm and 1.3 mm, and they end in short pinnule-free tips which are about as long and as thick as the pinnules (Fig.32, D–F). Some meristic data on the population are given Table 24.

The thorax is somewhat wider in specimens that had been accidentally removed from their tubes prior to fixation (Fig.32, G,H). Two clusters of prostomial ocelli are present. Ventral thoracic glands were not discernible.

The numbers of bayonet chaetae in 8 collar fascicles from different specimens, including a developing one deep within are: 4 in 1, 5 in 6, and 6 in 1. Their blades are moderately long and faintly serrated. The unserrated notch is about 1/3 the length of the blade. The tooth counts in the above 40 bayonet chaetae are: 3 in 18 (Fig.32,I,L), 4 in 17 (Fig.32, J,M), 5 in 1 (Fig.32, K), and indeterminate in the remaining 4. The usual number of teeth is, therefore, 3 or 4. In some chaetae two teeth may be large, while the third is much smaller (Fig.32,I).

Thoracic uncini (Fig.32, N) bear 4–5 teeth in a single row. Anterior abdominal uncini (Fig.32, O) are similar, with 4–6 teeth. Posterior abdominal uncini bear 1–3 teeth in a single row anteriorly, followed by a rasp-shaped cluster of smaller teeth posteriorly (Fig.32, Q). In the intermediate region there is a gradual reduction of the number of anterior teeth in the single row and a corresponding increase in the posterior cluster (Fig.32, P).

ETYMOLOGY. Renamed after its discoverer, D. Straughan.

HABITAT AND DISTRIBUTION. *S. minuta* occurs in shallow water, where it may form 'dense mats on the sheltered side of vertical rocks near L.W.M.' (Straughan, 1967).

It has hitherto been reported only from the type locality, Port Douglas, Queensland.

DISCUSSION

Spiraserpula Regenhardt 1961 differs from the remaining genera of its clade, namely *Serpula* Linnaeus 1758, *Hydroides* Gunnerus 1768 and *Crucigera* Benedict 1887, with regard to an important character, namely, the presence of ITS. In addition, the worm lacks an apron. The tubes of the other three genera lack ITS and, with a few exceptions, their worms possess an apron.

Straughan (1967) erected the the genus *Pseudoserpula* for *P. rugosa* (type species) and *P. minuta*, believing an operculum to be absent in both, and distinguished between them on the grounds that the former possessed a pair of pseudopercula (= rudimentary opercula) which were said to be absent in the latter. Ten Hove and Jansen-Jacobs (1984:162–165)

synonymized *Pseudoserpula rugosa* Straughan, 1967, with *Crucigera inconstans* Straughan, 1967, stating that the type of *Pseudoserpula* is a pseudoperculate individual of *C. inconstans*, but the evidence was incomplete. Moreover, there still remained the problem of the actual generic identity of *P. minuta* Straughan, 1967. Hence it was considered necessary to re-examine the types of *P. rugosa* and *P. minuta* and compare them with other collections, including those of *Crucigera inconstans*.

The holotype of the nominal species *Pseudoserpula rugosa* (AM W4027) yielded the following data: The tube is white, 2.0 mm in external diameter, and has conspicuous transverse wrinkles (Fig. 33, A–C). It lacks ITS. An operculum is absent, but a rudimentary operculum is present on each side (Fig. 33, C). An apron is present (Fig. 33, B). The bayonet chaetae typically possess two conical teeth on the basal boss, as seen in developing chaetae deep inside the fascicle (Fig. 33, H, I); one of the conical teeth may be smaller than the other or abraded in the older chaetae (Fig. 33, D–F). A short, unserrated notch is present; the chaetal shaft is smooth below the teeth.

Additional material of *Crucigera inconstans* (NSW, Sandy Beach, 21 km N. of Coffs Harbour, legit H. A. ten Hove, 27.iv.1986, Stn. 38 [8 specimens, ZMA V. Pol. 3741] and Sydney, Long Reef, intertidal rockpools, legit H. A. ten Hove and P. Hutchings, 29.iii.1986, Stn 30. [1specimen, ZMA V. Pol. 3740]) gave the following data: The tube is smooth and has transverse wrinkles (Fig. 33, J). Only three specimens, two from Sandy Beach and one from Long Reef, possess opercula; the remaining five only rudimentary opercula. The opercula (Fig. 33, J–L, S–V) agree fully with Straughan's description and figures of *C. inconstans*. The bayonet collar chaetae (Fig. 33, M–P) agree with those of the holotype of *Pseudoserpula rugosa*. The rudimentary opercula show different stages of development: both club-shaped, with somewhat tapering ends in the holotype (Fig. 33, C); one long and tapering, the other more bulbous (Fig. 33, W); and a clearly developing operculum (Fig. 34, A). While the holotype of *Crucigera inconstans* has 10 or 11 pairs of radioles (Straughan, 1967), an operculate individual in our material shows 15/16. The bayonet chaetae (Fig. 34, D–M) are similar, although they may occasionally possess a small third tooth (Fig. 34, J). A well developed apron is present in non-operculate and operculate specimens (Fig. 34, B), and in the holotype of *P. rugosa* (Fig. 33, B).

Some of the specimens bearing rudimentary opercula have regenerating radioles and/or operculum, which appear to have been nipped off on one side or the other (Figs. 33, W; 34, C). In one of the operculate specimens too some of the radioles are regenerating (Fig. 33, J). It appears, therefore, that opercula and radioles in *Crucigera inconstans* are favoured as food by certain predators. Whether this is the sole reason for a large number of specimens possessing only rudimentary opercula or not, has to be determined through further studies. It is worth noting, however, that the radioles of both sides in the holotype of *Pseudoserpula rugosa* are disproportionately small for the size of the worm, and show every indication of being in a state of regeneration (Fig. 33, B, C).

Meanwhile, *Pseudoserpula minuta* Straughan, 1967, lacks an apron and has ITS and, therefore, belongs to the genus *Spiraserpula* Regenhardt, 1961.

Another nominal genus, *Protoserpula* Uchida, 1978, needs to be discussed. Its original description does not mention if and where any material has deposited. It is not in the National Science Museum, Tokyo, and other efforts to obtain it were unsuccessful. Among the generic characters mentioned are the following: An operculum is absent, the number of thoracic chaetigers is 9 or 10, and capillary chaetae are absent towards the posterior end of the abdomen. The latter is emphasized in the statement 'All the species of *Serpula* and its related genera have their long hair-like abdominal posterior segments, but the new genus has not such kind of setae in abdomen' (Uchida, 1978: p. 23).

The more important characters described under *P. pacifica*, the type species, are as follows: 'Tube calcareous white opaque, cylindrical form, attached throughout its length, curved irregularly . . . Operculum absent. Branchiae consisting of 5 pairs of filaments and a pair of palpi. . . The ventral-most one pair of branchiae are much reduced (0.3 mm long). . . The thoracic membrane developed in the anterior region but suddenly reduced in width from the 5th segment, and it becomes to continue to the abdominal body surface without any structures in the last thoracic segment. Abdomen . . . consisting of about 20 setigerous segments, 2.5 mm long and 0.2 mm wide. . . Bayonet-shaped seta has a basal process with about 8 large teeth arranged into a circle. . . Each abdominal segment has 1–3 spatulate setae and 8–11 uncini on one side. . . The spatulate setae arranged to the last setigerous segment, and without substitution to the long hair-shaped setae as occurred in every species in *Hydroides*, *Serpula*, *Vermiliopsis*, and other many genera' (Uchida, 1978, p. 23–24).

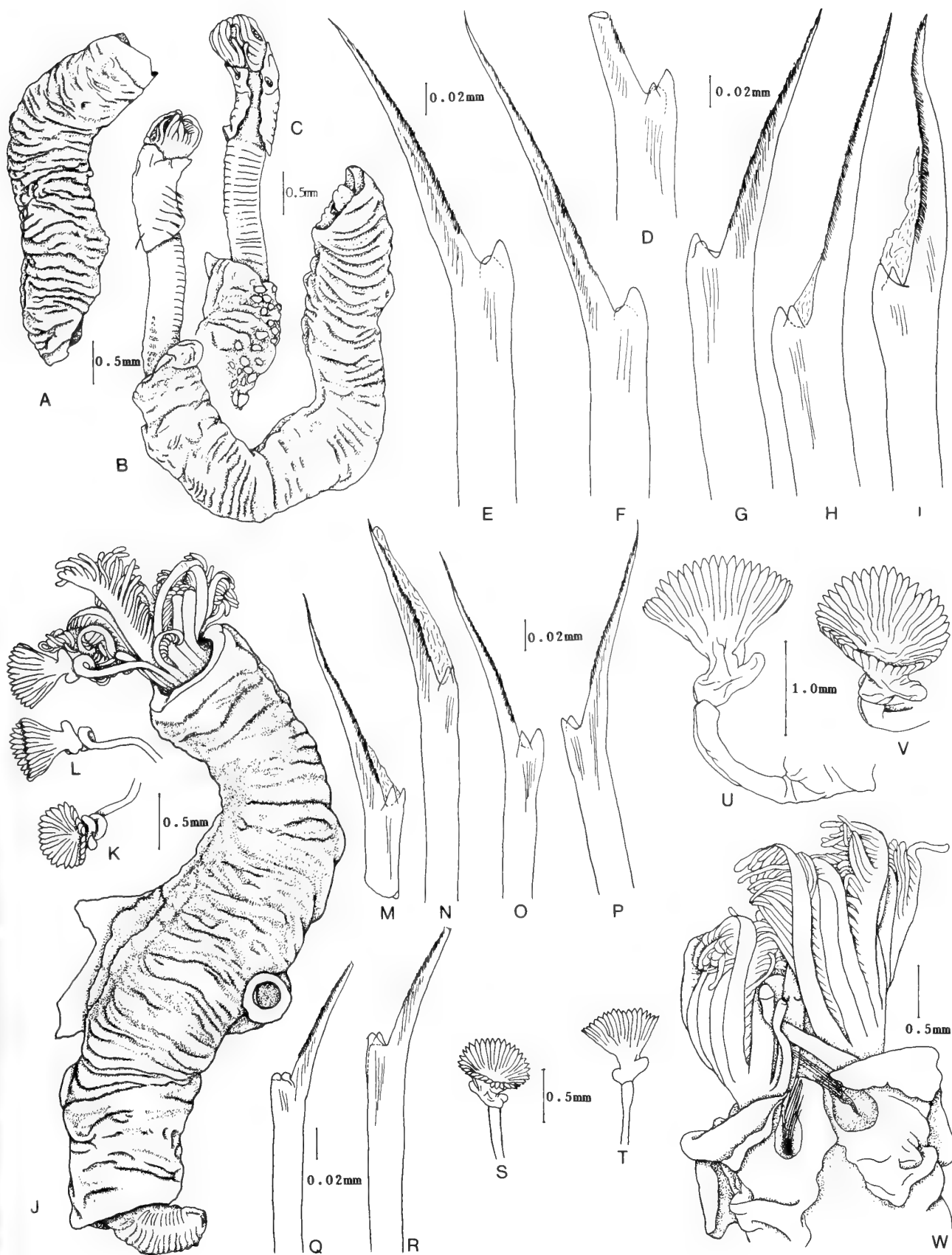
Protoserpula appears to be based on a juvenile serpulid (ten Hove, 1984, p. 193). A juvenile specimen would not be sound for erecting a genus since the adult characters could be different, particularly with regard to the presence or absence of an operculum.

In the development of operculate serpulids, the operculum appears after a certain number of radioles have already been formed (ten Hove 1984, p. 183, and Fig. 3). This appears to be in keeping with the greater importance of feeding and respiration over closure of the tube against predators at this stage. The dorsalmost pair of radioles remains simple and palp-shaped, and forms the lateral appendages of the dorsal lip (mouth palps). In this process they may decrease in size. The operculum develops as a modification of the second most dorsal radiole of one side.

As seen from the species of *Spiraserpula* described in this account, some possess an operculum, some may or may not possess one, and others lack one but possess a rudimentary operculum on each side. Some agree with regard to the number of radioles, but none of them show palps.

It appears unlikely that rudimentary opercula (=pseudo-percula) were mistaken for 'a pair of palpi' since, in the same paper, Uchida clearly distinguishes between pseudo-

Fig. 33 *Crucigera inconstans* Straughan, 1967. A–I, From holotype of *Pseudoserpula rugosa* Straughan, 1967, with only rudimentary opercula. A, Anterior part of tube. B & C, Worm within posterior part of tube, showing apron (B), presence of rudimentary opercula (=pseudo-percula, C). D–I, Bayonet chaetae. J–W, *Crucigera inconstans* Straughan, 1967 from Long Reef, Sydney. J & K, Operculate specimen within its tube and three views of its operculum. M–R, Bayonet chaetae from same fascicle, M & N newly formed deep within fascicle. S & T, Two views of small operculum. U & V, Two views of large operculum. W, Anterior end of large non-operculate specimen with two rudimentary opercula.



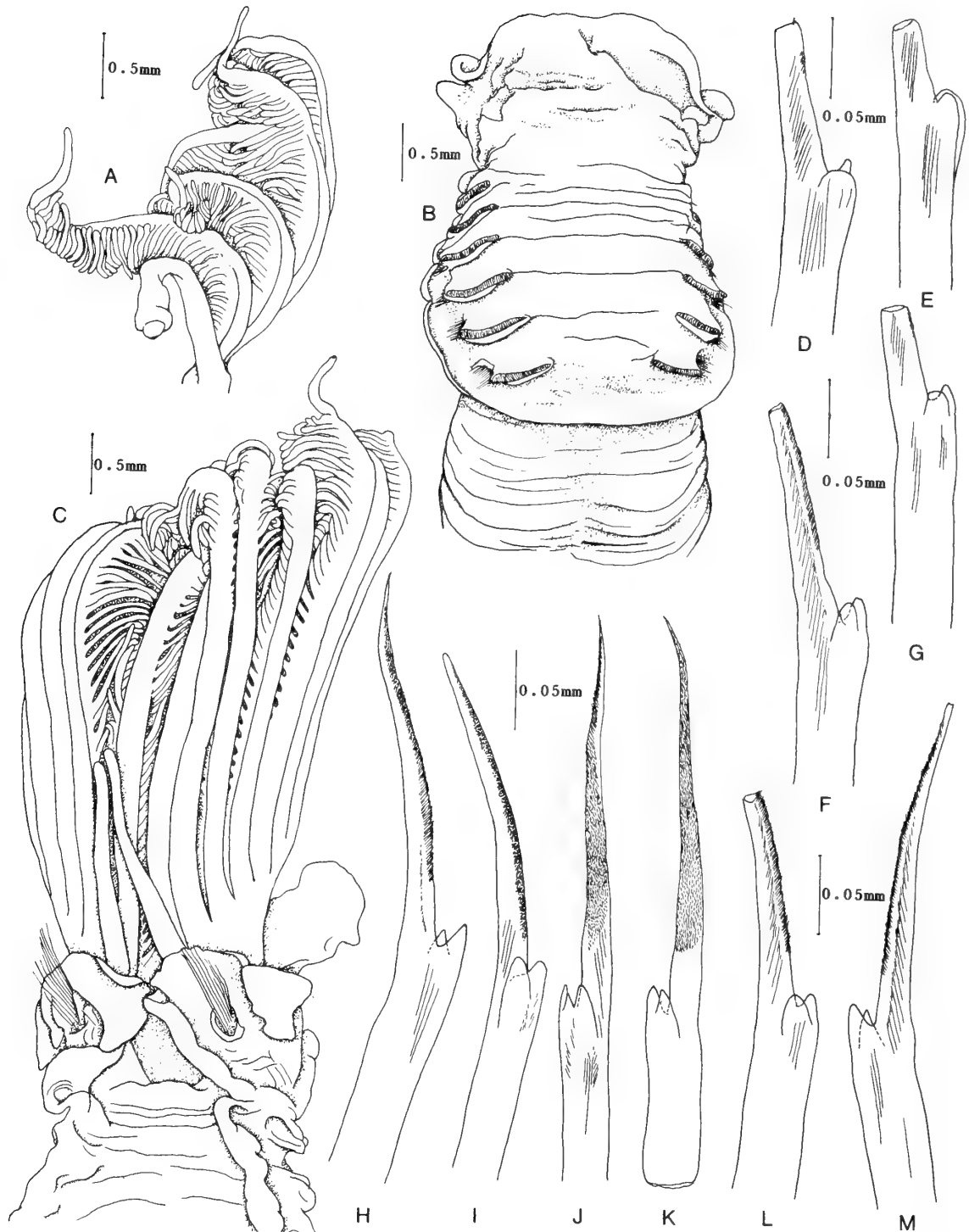


Fig. 34 *Crucigera inconstans* Straughan, 1967. A-M, From Sandy Beach, 21 km from Coff's Harbour. A, Right radioles of non-operculate specimen with rudimentary, but developing, operculum. B, Ventral view of large specimen showing apron. C, A large non-operculate individual with rudimentary opercula. D-M, Bayonet chaetae from the same fascicle of a large non-operculate specimen.

percula and opercula while defining the genera *Serpula*, *Crucigera*, *Hydroides* and *Protohydroides*. However, there is some inconsistency in terminology since he explicitly refers to the 'much reduced ventral most one pair of branchiae', and branchiae are also referred to as 'filaments' (= radioles). There is, therefore, room for doubt, and one

might infer that his 'palpi' are located on the dorsal side, and may actually be elongated rudimentary opercula.

The condition of the thoracic membranes in *P. pacifica* is not clear from the description. They sharply decrease in width posteriorly from the 5th chaetiger onwards and are insignificant or lacking as they approach the end of the thorax.

A range of specimens, including very small ones (Table 25), were covered under the species of *Spiraserpula* described in the present paper. The nominal species *P. pacifica*, therefore, has the same number of abdominal segments as the smallest juvenile among the other three species. The anterior abdominal chaetae of *Serpula* and related genera are frequently described as being trumpet-shaped or flat trumpet-shaped in serpulid literature. Uchida characterizes *P. pacifica* as lacking capillaries, but having spatulate chaetae in the terminal abdominal segments. However, all the species described in the present paper, including juveniles, possess capillary chaetae in the terminal abdominal segments, although there may occasionally be an individual in which they are lost (see condition in *S. singularis* sp. nov.).

Table 25 Some abdominal characters of the smallest juveniles of three new species, compared with those of *Protoserpula pacifica*.

Species	TL (mm)	Length of abdomen (mm)	No. of Abdom. segs.	Capillaries from
<i>S. caribensis</i>	3.7	2.0	20	16
<i>S. zibrowii</i>	3.4	2.1	27	19
<i>S. capeverdensis</i>	2.4	2.2	29	21
<i>Protoserpula pacifica</i>	5.1	2.5	20	—

The bayonet collar chaetae are similar to those of some species of *Spiraserpula*, but such chaetae are also found in *Serpula* sensu stricto species, such as *Serpula japonica* Imajima, 1979. It is not known whether *Protoserpula* possesses ITS or not, but they had also been overlooked until now in *S. massiliensis* (Zibrowius, 1968), *S. lineatuba* (Straughan, 1967), and *S. minuta* (Straughan, 1967).

It appears, therefore, that *Protoserpula pacifica* was a juvenile serpulid, and its true identity can only be established with more studies to determine the following: Whether it has a pair of true palps and an apron; if so, it does not belong to *Spiraserpula*. If, however, it has rudimentary opercula and ITS, and lacks an apron, it is likely to belong to *Spiraserpula* Regenhardt, 1961, which has priority over *Protoserpula* Uchida, 1978.

PHYLOGENY

Spiraserpula Regenhardt, 1961, is a member of the *Serpula*/*Crucigera*/*Hydroides* clade. A cladistic analysis of *Spiraserpula* Regenhardt, 1961, based on the above species (Hove & Pillai) was presented at the Fourth Polychaete Conference, and the paper is due to be published.

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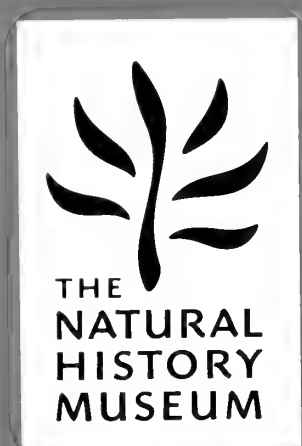
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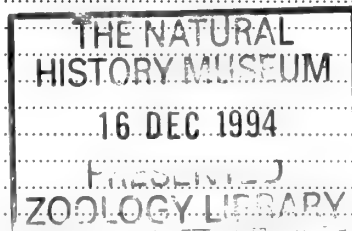
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SYNOPSIS. Ten genera, including three new genera, *Crassarietellus*, *Campaneria* and *Paraugaptiloides*, of the family Arietellidae (Copepoda: Calanoida) are newly defined or redefined with special reference to the genital systems of the females and fusion patterns and armature elements of appendages. The present study revealed that the single specimen reported as the male of *Sarsarietellus abyssalis* (Sars, 1905) represents a new genus, *Crassarietellus*, and that *Paraugaptilus mohri* Björnberg, 1975 belongs to the genus *Arietellus*. Ancestral and derived states and character transformations of the genital systems and the appendages in the family are discussed. A cladistic analysis for all 10 genera except for *Rhapidophorus* revealed that the Arietellidae consists of two lineages, the *Crassarietellus*-*Paramisophria*-*Pilarella*-*Metacalanus*-group and the *Campaneria*-*Sarsarietellus*-*Paraugaptiloides*-*Scutogerulus*-*Paraugaptilus*-*Arietellus*-group. The deep-sea hyperbenthic genera *Crassarietellus* and *Campaneria* are the most plesiomorphic in each group, and the shallow-water hyperbenthic/epipelagic/cave-living *Metacalanus* and the bathypelagic *Arietellus* and *Paraugaptilus* are relatively apomorphic.

INTRODUCTION

The family Arietellidae Sars, 1902 has been regarded as one of the most primitive families in the Calanoida based on the segmentation of appendages and the genital systems (Andronov, 1974; Park, 1986; Huys & Boxshall, 1991). The Arietellidae had hitherto accommodated the following eight genera: *Rhapi-*

dophorus Edwards, 1891, *Arietellus* Giesbrecht, 1892, *Paramisophria* T. Scott, 1897 (= *Parapseudocyclops* Campaner, 1977), *Metacalanus* Cleve, 1901 (= *Scottula* Sars, 1902), *Paraugaptilus* Wolfenden, 1904, *Scutogerulus* Bradford, 1969, *Sarsarietellus* Campaner, 1984, and *Pilarella* Alvarez, 1985. The genus *Phyllopus* Brady, 1883 was separated by Brodsky (1950) who proposed placing it in a new subfamily; it was later removed from the Arietellidae and placed in its own family, the Phyllopodidae

Table 1 Sampling date, locality, depth and gear used for arietellid collection.

Species	Sex	Number of specimens	Date	Locality	Depth (m)	Gear	Remarks
<i>Crassarietellus huysi</i> ¹	♀	1	18 IV 1977	20°18.5'N, 21°41.2'W	3974–4036	RMT8	5–20 m off bottom
	♀	2	18 IV 1977	20°20.8'N, 21°53.0'W 20°19.7'N, 21°51.3'W 20°18.4'N, 21°40.5'W	4008–4060	RMT8	5–20 m off bottom
<i>Crassarietellus</i> sp. ²	♂	1	24 VI 1908	38°02'N, 10°44'W	0–4800	Richard net	
<i>Campaneria latipes</i> ³	♂	1	4 X 1968	37°07'S, 177°14'E	1234–1260	Modified Menzies trawl	Some small stones
<i>Paragaptiloides magnus</i> ⁴	♂	1	11 X 1968	34°38'S, 174°36'E	1697	Modified Menzies trawl	
<i>Arietellus aculeatus</i>	♀	1	23 II 1979	15°00'–15°05'N 158°00'–158°01'W	400	IKMWT	
	♂	2	23 II 1979	15°10'–31°14'S 71°56'–71°58'W	400	IKMWT	
<i>Arietellus mohri</i> ⁵	♀	1	24 VI 1962	31°10'–31°14'S 71°56'–71°58'W	1932–3142	Phlenger corer	
<i>Arietellus pavoninus</i> ⁶	♀	1	28 XI 1965	28°05'N, 14°06'W	600–720	N113H	
<i>Arietellus plumifer</i>	♀	1	28 VI 1985	31°20'N, 25°17'W 31°18'N, 25°27'W	600–840	RMT1	
	♀ ⁶	1	26 XI 1965	28°07'N, 14°07'W	680–800	N113H	
	♂ ⁶	1	13 XI 1965	28°04'N, 14°12'W	360–410	N113H	
<i>Arietellus setosus</i> ⁶	♂	1	29 XI 1965	28°05'N, 14°10'W	50–85	N113H	
<i>Arietellus simplex</i> ⁶	♂	1	28 XI 1965	28°05'N, 14°06'W	750–900	N113H	
<i>Arietellus</i> sp. ⁶	♀	1	11 XI 1965	28°04'N, 14°11'W	460–510	N113H	
<i>Metacalanus</i> sp. 1	♀	4	23 V 1989	26°17.9'N, 126°54.2'E	167	Sledge-net	
	♀	1	23 V 1989	26°17.9'N, 126°54.2'E	167	Sledge-net	
<i>Metacalanus</i> sp. 2	♀	4	23 V 1989	26°17.9'N, 126°54.2'E	167	Sledge-net	
<i>Paramisophria giselae</i> ⁷	♀	2	3 IX 1970	23°19'S, 41°57'W	100	Plankton net adapted to dredge	
<i>Paramisophria japonica</i> ⁸	♀	1	23 V 1989	26°17.9'N, 126°54.2'E	167	Sledge-net	
<i>Paramisophria reducta</i> ⁹	♀	1	25 II 1984	Jameos del Agua	10–28	Plankton net	
<i>Paragaptilus buchani</i> ⁶	♀	1	16 XI 1969	17°41'N, 25°18'W	410–500	RMT1	
	♀	1	15 XI 1965	27°48'N, 13°55'W	450–510	N113H	
	♀	1	24 XI 1965	28°06'N, 14°08'W	775–830	N113H	
<i>Paragaptilus similis</i>	♀	1	21 I 1978	04°02'S, 150°00'W	275	IKMWT	
	♀	1	21 I 1978	04°02'S, 150°00'W	275	IKMWT	
<i>Pilarella longicornis</i> ¹⁰	♀	1	22 VI 1970	28°36'S, 47°55'W	135	Plankton net adapted to dredge	
<i>Scutogerulus pelophilus</i> ³	♀	1	10 X 1968	34°56'S, 175°23'E	1383–1397	Modified Menzies trawl	<i>Globigerina</i> Ooze
<i>Sarsarietellus abyssalis</i> ²	♀	1	4–5 VIII 1897	38°37'N, 28°14'W	1260	'Nasse'	

Sampling data after: ¹ Boxshall & Roe (1980); ² Sars (1925); ³ Bradford (1969); ⁴ Bradford (1974); ⁵ Björnberg (1975); ⁶ Currie et al. (1969); ⁷ Campaner (1977); ⁸ Ohtsuka et al. (1991); ⁹ Ohtsuka et al. (1993a); ¹⁰ Alvarez (1985).

(Campaner, 1977; Bowman & Abele, 1982).

Arietellids are widely distributed from neritic to oceanic waters and range vertically from the epipelagic zone to the bathypelagic hyperbenthic layer (Campaner, 1984). Recently, cave-living species of *Metacalanus* and *Paramisophria* have been discovered (Ohtsuka et al., 1993a). However, neither phylogenetic nor ecological studies on the family have been carried out in detail, partly because of the paucity of pelagic arietellids in the water column, and partly because of the lack of intense sampling effort in the hyperbenthic layers where many species are found.

Campaner (1984) first examined the relationships between arietellid genera. He divided them into two morphologically and ecologically different groups. The first group comprised *Arietellus*, *Paragaptilus* and *Scutogerulus*, which are characterized by a reduced female leg 5 and complex male leg 5, and are distributed in the bathypelagic or deep-sea hyperbenthic zones. The second group consisted of *Metacalanus*, *Paramisophria*, *Rhaphidophorus* and *Sarsarietellus* and was diagnosed by characters such as the relatively well developed leg 5 in the female (except for *Metacala-*

nus) and the simplified second exopod segments and reduction of endopod of leg 5 in the male. These are highly adapted hyperbenthic forms found in relatively shallow waters (<1000 m deep) or in epipelagic waters in neritic regions. However, Campaner's (1984) classification relied solely on the structure of the fifth legs although he recognized interspecific variation between congeners in leg characters.

The present paper describes a new arietellid genus collected from the deep-sea hyperbenthic community in the northeastern Atlantic, and establishes two new genera to accommodate previously known arietellids, the male of *Scutogerulus pelophilus* Bradford, 1969 and the male of *Paragaptilus magnus* Bradford, 1974. Revised diagnoses of all known arietellid genera, except for *Rhaphidophorus*, are given here together with supplementary descriptions. Character transformations of the genital systems and appendages of these arietellids are considered in detail. A cladistic analysis is employed to help clarify phylogenetic relationships between the arietellid genera.

Table 2 Characters used in the cladistic analysis for genera of the family Arietellidae. Codes 0 to 2 refer to transformation series of multi-state characters; 0: plesiomorphic state; 9: missing data.

1.	Gonopore and copulatory pore sharing common opening	yes/no	0/1
2.	Right and left copulatory pores	separate/fused	0/1
3.	Lengths of right and left antennules of female	equal/unequal	0/1
4.	Fusion of female antennular segments I-III and IV	separate/fused	0/1
5.	Fusion between female antennular segments XXIII and XXIV	separate/fused	0/1
6.	Aesthetasc present on female antennular segment IV	present/absent	0/1
7.	Aesthetasc present on female antennular segment VI	present/absent	0/1
8.	Aesthetasc present on female antennular segment VIII	present/absent	0/1
9.	Aesthetasc present on female antennular segment X	present/absent	0/1
10.	Aesthetasc present on female antennular segment XII	present/absent	0/1
11.	Modification of seta into process on male antennular segment XV	no/yes	0/1
12.	Fusion of male antennular segments XXI & XXII	separate/fused	0/1
13.	Seta adjacent to aesthetasc on male antennular segments II	present/absent	0/1
14.	Seta adjacent to aesthetasc on male antennular segment III	present/absent	0/1
15.	Modification of seta into process on male antennular segment XXII	no/yes	0/1
16.	Process on male antennular compound segment XXIV-XXV	no/yes	0/1
17.	Seta on first endopod segment of antenna	present/absent	0/1
18.	Proximal inner seta on mid-margin of second endopod segment of antenna	present/absent	0/1
19.	Vestigial element on second endopod segment of antenna	present/absent	0/1
20.	1-segmented, rudimentary mandibular endopod with 1 or 2 setae	present/absent	0/1
21.	Outer terminal seta on fifth exopod segment of mandible	normal/reduced	0/1
22.	Process on maxillulary praecoxal arthrite	present/absent	0/1
23.	Inner basal enditic seta of maxillule	present/absent	0/1
24.	Third seta of maxillulary endopod	present/absent	0/1
25.	Inner angle seta of maxillulary endopod	present/absent	0/1
26.	Distal seta on first on first praecoxal endite of maxilla	present/absent	0/1
27.	Reduction of seta a on sixth endopod segment of maxilliped (length of seta at most as long as the segment)	no/yes	0/1
28.	Reduction of seta b on sixth endopod segment of maxilliped (length of seta at most as twice as long as segment)	no/yes	0/1
29.	Proximal spine on outer margin of third exopod segment of leg 1	present/absent	0/1
30.	Inner coxal seta of leg 4	present/absent	0/1
31.	Fusion between endopod and basis of female leg 5	separate/fused	0/1
32.	Inner margin of endopod of female leg 5 with proximal (seta A) and distal (seta B) setae	A + B present/ A or B absent	0/1
33.	One seta (A or B) on inner margin of endopod of female leg 5	present/absent	0/1
34.	Inner angle seta on distal margin of endopod of female leg 5	present/absent	0/1
35.	Exopod segment of female leg 5	partly defined/ unsegmented/absent	0/1/2
36.	Spine (element d) on outer distal angle of exopod of female leg 5	present/absent	0/1
37.	Left endopod of male leg 5 (including incomplete fusion)	2-segmented/ 1-segmented/absent	0/1/2
38.	Right endopod of male leg 5	1-segmented/absent	0/1
39.	Seta c on third exopod segment of left male leg 5	present/absent	0/1
40.	Setae e and f of left male leg 5 transformed into bifid process	no/yes	0/1
41.	Third exopod segment of left male leg 5 rotated so that vestigial outer margin elements now on inner surface	no/yes	0/1
42.	Seta f on third exopod segment of right male leg 5	well developed/minute	0/1
43.	Seta c on third exopod segment of right male leg 5	present/absent	0/1
44.	Fusion between coxa and basis of right male leg 5	separate/fused	0/1

Table 3 Character matrix for analysis using PAUP 3.0.

<i>Crassarietellus</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	9	9	0		
<i>Paramisophria</i>	1	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0		
<i>Metacalanus</i>	1	0	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	1	0	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	2	1	1	0	0	0	1	0	
<i>Arietellus</i>	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	1	0	1	1	1	
<i>Paraugaptilus</i>	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	2	2	1	0	1	1	1	1	1		
<i>Scutogerulus</i>	0	0	0	0	0	1	0	0	0	0	9	9	9	9	9	9	1	0	0	0	0	1	0	1	1	1	1	1	1	0	1	1	1	0	1	9	9	9	9	9	9	9		
<i>Sarsarietellus</i>	1	1	0	0	0	1	0	0	0	0	9	9	9	9	9	9	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	9	9	9	9	9	9	9		
<i>Pilarella</i>	0	0	1	1	0	1	1	0	0	0	9	9	9	9	9	9	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	9	9	9	9	9	9	9		
<i>Campaneria</i>	9	9	9	9	9	9	9	9	9	9	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	9	9	9	9	9	9	0	0	1	0	0	1	1	0	
<i>Paraugaptiloides</i>	9	9	9	9	9	9	9	9	9	9	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	9	9	9	9	9	9	0	0	0	1	1	1	1	1

MATERIALS AND METHODS

The present study is based on collections deposited in The Natural History Museum, London, the New Zealand Oceanographic Institute, the United States National Museum, Smithsonian Institution, the Zoological Museum, University of Oslo, the University of Sao Paulo, and Hiroshima University. Sampling data and locality are summarized in Table 1. Specimens, except for those previously mounted, were dissected and mounted in Gum-chloral and observed with a differential interference contrast microscope (Olympus BH-2). The genital double-somites of females of several species were observed with a scanning electron microscope (Hitachi S-800). The morphological terminology is based on Huys & Boxshall (1991). Type specimens of the new genera are deposited in The Natural History Museum and the New Zealand Oceanographic Institute.

Phylogenetic relationships between genera were analyzed using PAUP version 3.0 prepared by D. Swofford, Illinois Natural History Survey. The character matrix (Tables 2,3) summarizes the character distributions among the 10 genera available for study. A multistate scoring system was employed and missing characters were scored 9. A hypothetical composite ancestor was included in the analysis which scored 0 for all characters. The options employed in the analysis were Branch and Bound, which guaranteed to find all the most parsimonious trees, and the MINF optimisation, which assigns character states so that the f-value is minimized. All characters were set as irreversible using the Camin-Sokal option.

The abbreviations used in the text and figures 1 to 37 are as follows: cd: copulatory duct; cp: copulatory pore; g: gonopore; o: oviduct; rd: receptacle duct; s: spermatophore remnant; sr: seminal receptacle.

SYSTEMATICS

Family Arietellidae Sars, 1902

DIAGNOSIS (emend.) Female. Body of variable size (from ca. 0.8 to 7 mm), relatively robust, rarely compressed. Cephalosome and first pedigerous somite separate or weakly fused; fourth and fifth pedigerous somites completely fused. Cephalosome round or pointed at apex; rostrum produced ventrally, with pair of filaments. Posterior corner of prosome sharply or weakly produced, with or without dorsolateral and/or ventrolateral process. Urosome comparatively short, 4-segmented; genital double-somite with single or paired gonopores and copulatory pores; gonopore(s) located ventrolaterally or ventrally, with or without opercular plate; copulatory pore sharing common opening with gonopore or separate from gonopore, located ventro-medially or -posteriorly, rarely ventrally on right side; seminal receptacles usually paired, rarely left receptacle entirely lacking. Egg-sac present or absent. Caudal rami well defined, symmetrical or slightly asymmetrical, relatively short, with vestigial seta I, well developed or reduced setae II–III, well developed setae IV–VI and small seta VII.

Antennules symmetrical or asymmetrical, longer on left side than on right, sometimes differing in fusion pattern and

armature; 16- to 22-segmented; segments I to III, rarely up to VI fused; segments X to XII more or less fused; segments XXIII and XXIV separate or fused; segments XXV and XXVI completely or incompletely fused; segments II, XXII–XXIV, XXVI and XXVII lacking aesthetasc; segment IV, VI, VIII–X, XII and XIII with or without aesthetasc; segment XIII with 1 or 2 setae; compound segment XXVI–XXVIII with 8 or 9 elements; posterior margin of proximal segments fringed with row of setules or not. Antenna: basal seta present; both rami separate from basis; endopod 2-segmented, first segment with 0–1 inner seta at midlength, second segment elongate, with 1–3 inner setae medially and 5 or 6 setae terminally; exopod indistinctly 6- to 10-segmented, ancestral segments I–III and IX unarmed. Mandible: gnathobase well chitinized, with 3 or 4 sharp teeth; endopod rudimentary, 1-segmented with 1 or 2 setae terminally or completely absent; first exopod segment with normal or reduced seta, fifth segment carrying 2 setae, one of which sometimes vestigial. Maxillule: praecoxal arthrite with 0–6 elements; coxal endite with 1 seta or unarmed; coxal epipodite carrying 5–9 setae; inner basal seta representing endite vestigial or absent; endopod bulbous, 1-segmented, with 0–3 setae or completely incorporated to basis; exopod lobate, bearing 3 long setae. Maxilla well developed; first praecoxal endite with 1 or 2 setae and 1 vestigial element, second praecoxal endite having 1 or 2 setae; first and second coxal endites each with 2 setae; basal spine stout, spinulose or bare; endopod 4-segmented, with chitinized long setae, setal formula 1,3,2,2. Maxilliped elongate; syncoxa with 1 medial and 2 terminal setae; basis with patches of setules or spinules and 2 setae medially; endopod 6-segmented, first segment almost fully incorporated into basis, setal formula 1,4,4,3 (rarely 2),3 (rarely 2),4, sixth segment with 2 outermost terminal setae (setae 'a' and 'b', see Fig. 5C) reduced or not.

Legs 1–4 with distinctly 3-segmented rami or, very rarely, with endopod segments of leg 1 incompletely fused. Seta and spine formula of legs 1–4 as shown in Table 4.

Leg 5 variable but not natatory, almost symmetrical; coxae and intercoxal sclerite separate or fused; basis and endopod separate or fused; endopod with 0–4 setae; exopod 1- to 3-segmented or completely fused with basis, carrying 0–5 elements.

Male. Body similar to that of female, but urosome 5-segmented. Left antennule geniculate, 16- to 20-segmented; segments I to IV fused; segments XI to XV more or less fused; segments XXI and XXII fused or rarely separate; segments XXIII and XXIV separate; segments XXV and XXVI completely or incompletely fused; segments II and III with 1 or 2 setae; segments X, XII–XIV and XX with anterior process; segments XIX and XXI with 2 processes; segment XIII with 0–1 seta; segments XV, XXII and XXIV with or without process; proximal segments often with row of setules along posterior margins. Mouthparts and legs 1–4 similar to

Table 4 Spine and seta formula of legs 1–4.

	Coxa	Basis	Exopod segment	Endopod segment
Leg 1	0–1	1–1	I–1;I–1;III,I,1,4	0–1;0–2;1,2,2
Leg 2	0–1	0–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4/3
Leg 3	0–1	0–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4/3
Leg 4	0–0/1	1–0	I–1;I–1;III,I,5	0–1;0–2;2,2,3/2

those of female or slightly different in armature elements of antennary second endopod segment and mandibular first exopod segment.

Leg 5 variable, but not natatory, almost symmetrical to strongly asymmetrical; coxae and intercoxal sclerite fused to form common base or separate; right basis sometimes fused with coxa; right endopod 1-segmented, bulbous or absent; right exopod distinctly or indistinctly 3-segmented, first and second segments each with seta on outer margin (rarely first segment unarmed), second segment with tuft of setules on inner distal angle of second segment, third segment with 0–3 elements terminally; left endopod 1- or 2-segmented, unarmed or completely absent; left exopod distinctly or indistinctly 3-segmented, first and second segments each with seta on outer margin, third segment with 1–3 elements terminally.

TYPE GENUS. *Arietellus* Giesbrecht, 1892.

REMARKS. The above diagnosis excludes *Rhapidophorus* Edwards, 1891, which was inadequately described and has never been redescribed. Although the family was briefly defined by Sars (1902), Rose (1933), Brodsky (1950) and Campaner (1977), the present amended definition includes new information on the genital systems of females and the armature elements on the appendages.

Genus *Crassarietellus* gen. nov.

DIAGNOSIS. Female. Body compact, prosome ovoid in dorsal view; cephalosome separate from first pedigerous somite; posterior corner of prosome produced posteriorly to form rounded lobe. Urosome short, at most one-third as long as prosome; genital double somite wider than long, with pair of gonopores ventrolaterally and paired copulatory pores each located beneath ventral projection; anal operculum not developed; caudal rami symmetrical, longer than wide, with vestigial seta I and normally developed seta II.

Antennule symmetrical reaching to posterior end of second pedigerous somite, 22-segmented; segments I–III fused, with 7 setae and 2 aesthetascs; segments IV, VI, XII and XIII each with 2 setae and 1 aesthetasc; segments XXIII and XXIV separate; compound segment XXVI–XXVIII with 8 setae and 1 aesthetasc; posterior margin of ancestral segments I to XIII fringed with long setules; segments IV–VIII with transverse row of long setules along distal end of segment. Antenna: first endopod segment with medial inner seta; second segment bearing 3 midlength and 5 terminal setae; exopod indistinctly 10-segmented exopod. Mandibular gnathopod with tuft of setules at midlength and 3 teeth on cutting edge. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long.

Maxillule: praecoxal arthrite with 5 stout, serrate spines and 1 process; coxal epipodite having 6 setae; coxal endite bearing long seta; second basal endite with vestigial seta; endopod rudimentary, 1-segmented with 2 setae. Maxilla: first syncoxal endite with 2 setae and vestigial element; second syncoxal endite with 2 setae; basal endite carrying stout spine with row of spinules medially. Maxilliped with second to sixth endopod segments bearing 4, 4, 3, 3 and 4 setae, respectively; innermost seta on fourth and fifth endopod segments not reduced; setae a and b on sixth endopod segment not reduced.

Leg 1 bearing 2 outer lateral spines on third exopod

segment. Leg 5 having distinctly 1-segmented, rudimentary endopod with 2 setae and indistinctly 3-segmented exopod with 3 outer lateral and 2 terminal spines.

Male. Left antennule geniculate, 19-segmented; segments I–IV fused, with 9 setae and 4 aesthetascs; segments XXI and XXII fused; segments I to X fringed with setules along posterior margin; segments IV to VIII with transverse row of setules as in female. Mouthparts and legs similar to those of female.

Leg 5 with coxae and intercoxal sclerite incompletely fused to form common base; coxa separate from basis. Right leg lacking endopod; exopod, at least 2-segmented, first segment with outer spine on distal corner. Left leg: endopod incompletely 2-segmented, first segment expanded, second segment small, semispherical; exopod distinctly 3-segmented, first segment with spine on outer corner, second segment expanded, bearing outer spine at midlength, third segment small, having 2 small outer setules and chitinized, long terminal seta.

TYPE SPECIES. *Crassarietellus huysi*, gen. et sp. nov.

Other species. *Crassarietellus* sp. based on a male which was erroneously assigned to *Scottula abyssalis* Sars, 1905 by Sars (1924, 1925).

REMARKS. Sars (1924, 1925) assigned one male collected from off Lisbon to *Scottula abyssalis* Sars, 1905, the female of which was captured off the Azores. However, this male should be included in the new genus *Crassarietellus* based on the similarities of the mouthparts: the indistinctly 10-segmented antennary exopod (compare Fig. 1F with Fig. 7D); 5 serrate spines and a process on the praecoxal arthrite and 6 setae on the coxal epipodite of the maxillule (Figs 5A, 8A); 2 non-reduced setae on the sixth endopod segment of the maxilliped (Figs 5C, 8E). Additionally, a transverse row of setules is present, on each of the antennular segments IV to VIII in the male (Fig. 7A), that is found only in the genus *Crassarietellus*. The ornamentation of the appendages of the male, such as the many tiny spinules along the outer margin of the mandibular palp and the stout, outer processes on the exopod segments of legs 1 to 4, also supports the proposal to place the male in *Crassarietellus*. The right leg 5 of the male lacks distal exopod segment(s), a condition which Sars (1924, 1925) misinterpreted as '1-segmented left' exopod.

ETYMOLOGY. The new generic name *Crassarietellus* (Latin *crassus* meaning thick) refers to the ovoid, compact body form of the new genus. The specific name is named in honour of Mr. Rony Huys.

ECOLOGICAL NOTE. The type species of the new genus was found in near-bottom samples taken at depths of 3974–4060 m. The plump body and the relatively short antennules indicates that the new genus is hyperbenthic.

Crassarietellus huysi gen. et sp. nov. (Figs 1–6)

MATERIAL EXAMINED. 3 ♀♀.

TYPES. Holotype: ♀, 18 IV 1977, North Atlantic (off western Africa), 20°8.5'N, 21°1.2'W–20°20.8'N, 21°53.0'W, 3974–4036 m in depth, dissected and mounted on slides, prosome and urosome preserved in 70% ethanol, BM(NH) 1993.424. Paratype 1: ♀, 18 IV 1977, 20°19.7'N, 21°51.3'N–20°18.4'N, 21°40.5'W, 4008–4060 m in depth, dissected and mounted on slides, prosome preserved in 70%

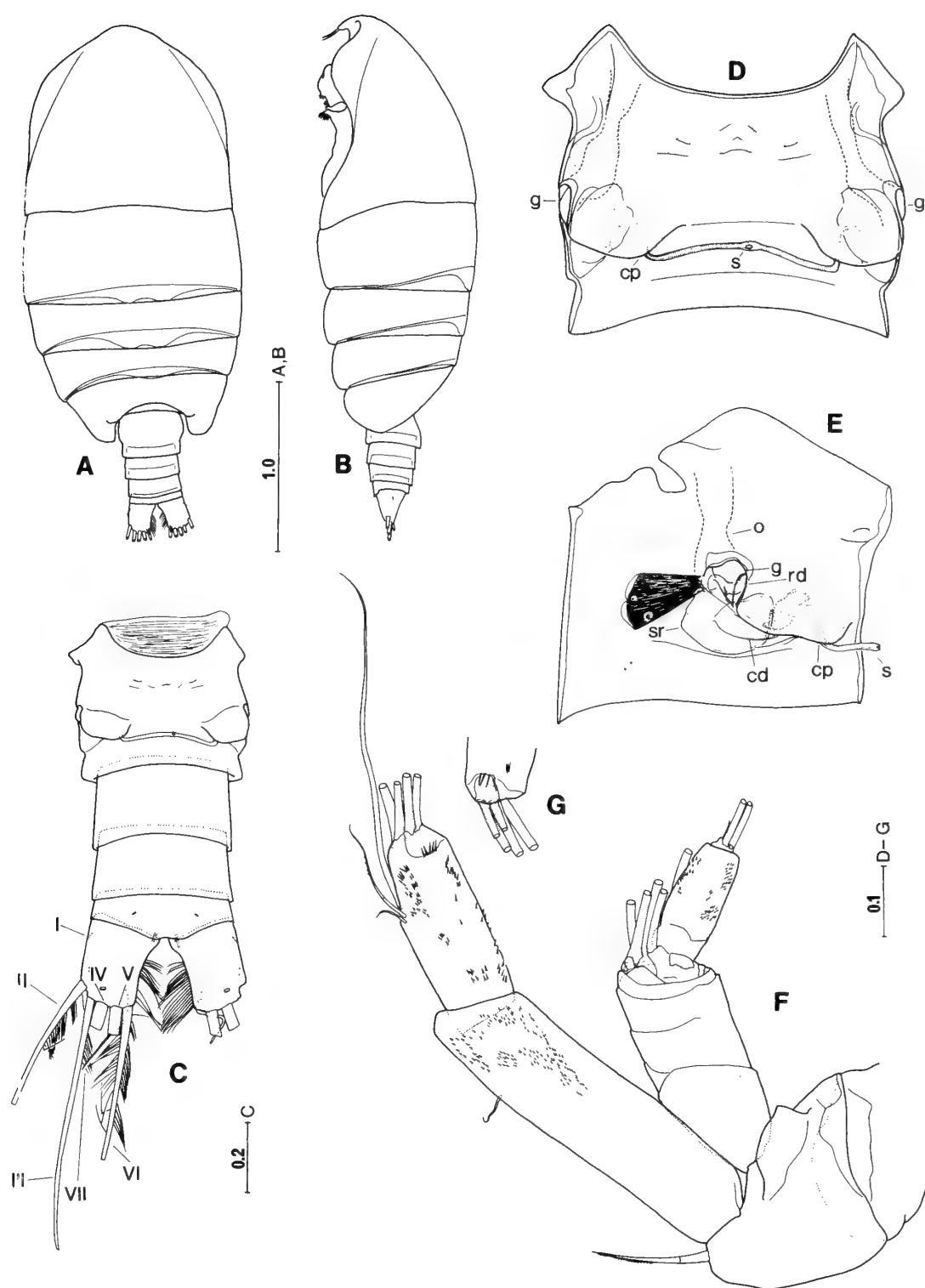


Fig. 1. *Crassarietellus huysi* gen. et sp. nov., female (holotype: F,G; paratype: A-E). A, Habitus, dorsal view; B, Habitus, lateral view; C, Urosome, ventral view; D, Genital double-somite, ventral view; E, Genital double-somite, lateral view, cd: copulatory duct; cp: copulatory pore; g: gonopore; rd: receptacle duct; o: oviduct; s: spermatophore remnant; sr: seminal receptacle; F, Antenna, one terminal seta on second endopod segment missing; G, Terminal part of second endopod of other antenna. Scales in mm.

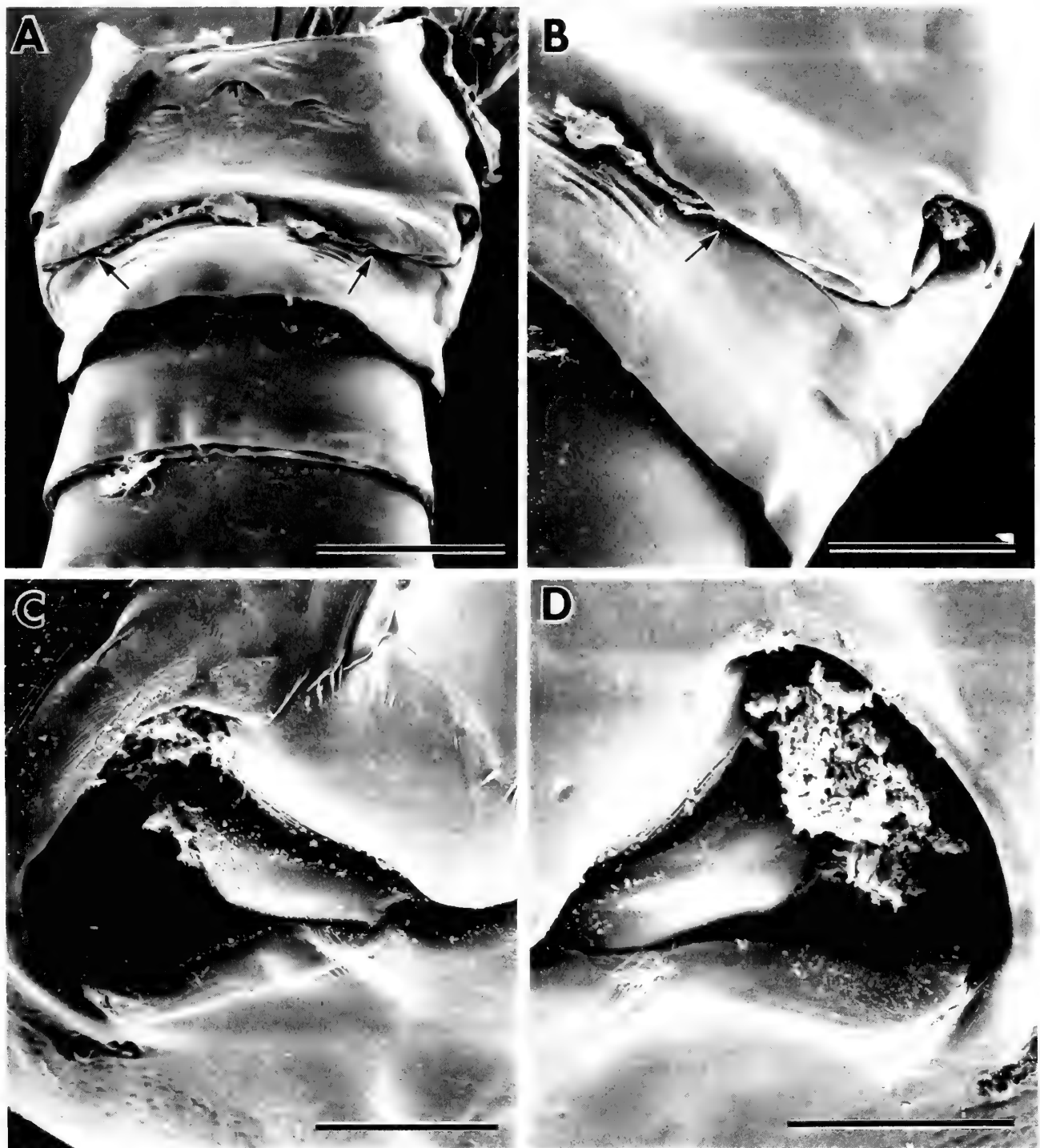


Fig. 2. *Crassarietellus huysi* gen. et sp. nov., female. SEM micrographs of genital double-somite of female. A, Genital double-somite, ventral view, scale bar = 200 μ m (arrows indicating positions of copulatory pores); B, Gonopore and copulatory pore (indicated by arrow), scale bar = 100 μ m; C, Right gonopore, scale bar = 30 μ m; D, Left gonopore, scale bar = 30 μ m.

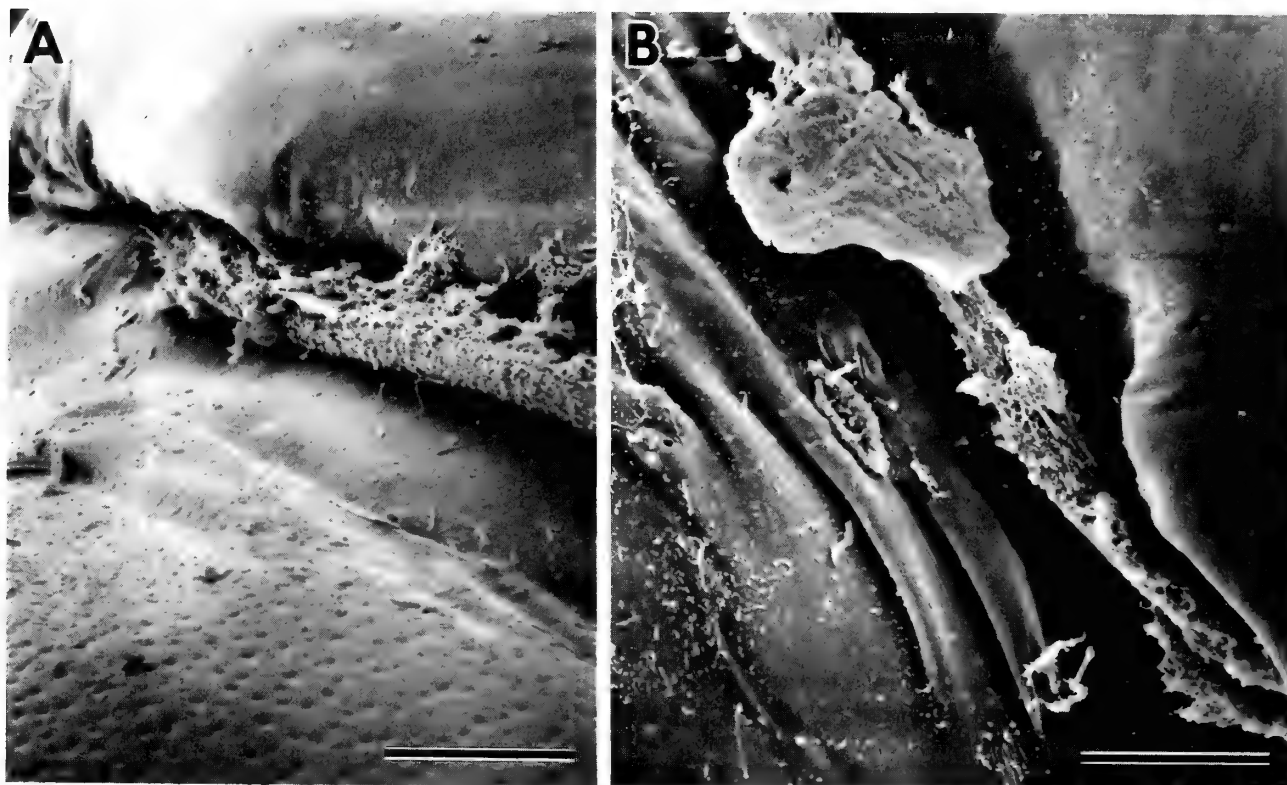


Fig. 3 *Crassarietellus huysi* gen. et sp. nov., female. SEM micro-graphs of remnant of spermatophore attached to genital double-somite of female. A, Spermatophore remnant penetrating copulatory pore, scale bar = 20 μ m; B, Spermatophore remnant, scale bar = 20 μ m.

ethanol, BM(NH) 1993. 425. Paratype 2: ♀, the same collection date and locality as in paratype 1, only legs 2 and 3 dissected and mounted on glass slides, urosome mounted on stub for SEM examination, prosome preserved in 70% ethanol, BM(NH) 1993. 426.

BODY LENGTH. 3.88 mm (holotype); 3.88, 3.85 mm (paratypes).

DESCRIPTION. Female. Body (Fig. 1A,B) oval in dorsal view. Cephalosome and first pedigerous somite separate; fourth and fifth pedigerous somites completely fused; posterior corner of prosome produced posteriorly into rounded lobe directed backwards, reaching half length of genital double-somite. Urosome (Fig. 1C) 4-segmented, one-third as long as prosome; genital double-somite (Figs 1D,E,2A,B) wider than long; pair of medial gonopores (Fig. 2C,D) located ventro-laterally near mid-level of double-somite; paired copulatory pores posterior to gonopores, each concealed beneath ventrolateral projection; remnants of divergent fertilization tubes of spermatophore (Fig. 3) still attached to genital double-somite of both paratypes, each connecting through posteroventral groove with copulatory pore beneath projection; copulatory duct swollen in ventrolateral projection, almost horizontal, extending to large seminal receptacle; 1 medial and 2 pairs of lateral shallow chitinized pits anteriorly; anal somite small, anal operculum not developed; caudal ramus (Fig. 1C) longer than wide, fringed with long setules along inner margin, with vestigial seta I and developed setae II to VI, seta VII originating dorsally near base of seta VI; inner margin near anus with

patch of minute spinules. Integument of body and appendages pitted.

Antennules (Fig. 4A-C) equal in length, distinctly 22-segmented, reaching to posterior end of second pedigerous somite; distal 2 segments incompletely fused; fusion pattern and armature as follows: I-III-7 + 2 aesthetascs, IV-2 + aesthetasc, V-2 + aesthetasc, VI-2 + aesthetasc, VII-2 + aesthetasc, VIII-2 + aesthetasc, IX-2 + aesthetasc, X-2 + aesthetasc, XI-2 + aesthetasc, XII-2 + aesthetasc, XIII-2 + aesthetasc, XIV-2 + aesthetasc, XV-2 + aesthetasc, XVI-2 + aesthetasc, XVII-2 + aesthetasc, XVIII-2 + aesthetasc, XIX-2 + aesthetasc, XX-2 + aesthetasc, XXI-2 + aesthetasc, XXII-1, XXIII-1, XXIV-XXVIII-12 + 2 aesthetascs. Segments I to XIII fringed with long setules along posterior margin; segments IV to VIII each furnished with transverse row of minute setules near posterior corner. Sutures between segments I to III weakly visible.

Antenna (Fig. 1F,G): coxa unarmed; basis with spinulose seta at inner angle; endopod 2-segmented, first segment with minute seta at three quarters length, covered with minute spinules distally, second with 3 setae of unequal lengths medially and 5 setae distally and sparsely covered by spinules; exopod indistinctly 10-segmented, second to fourth segments almost fused; armature as follows: 0,0,0,1,1,1,1,0,3; ninth segment sparsely ornamented with minute spinules.

Mandible (Fig. 4D): gnathobase heavily chitinized, ventro-medial margin with dense fringe of long setules; cutting edge with 3 acute teeth, dorsalmost of which bifid at tip; 2 patches of dagger-like spinules present dorsally; tuft of long setules present medially on knob; basis of palp with patches of

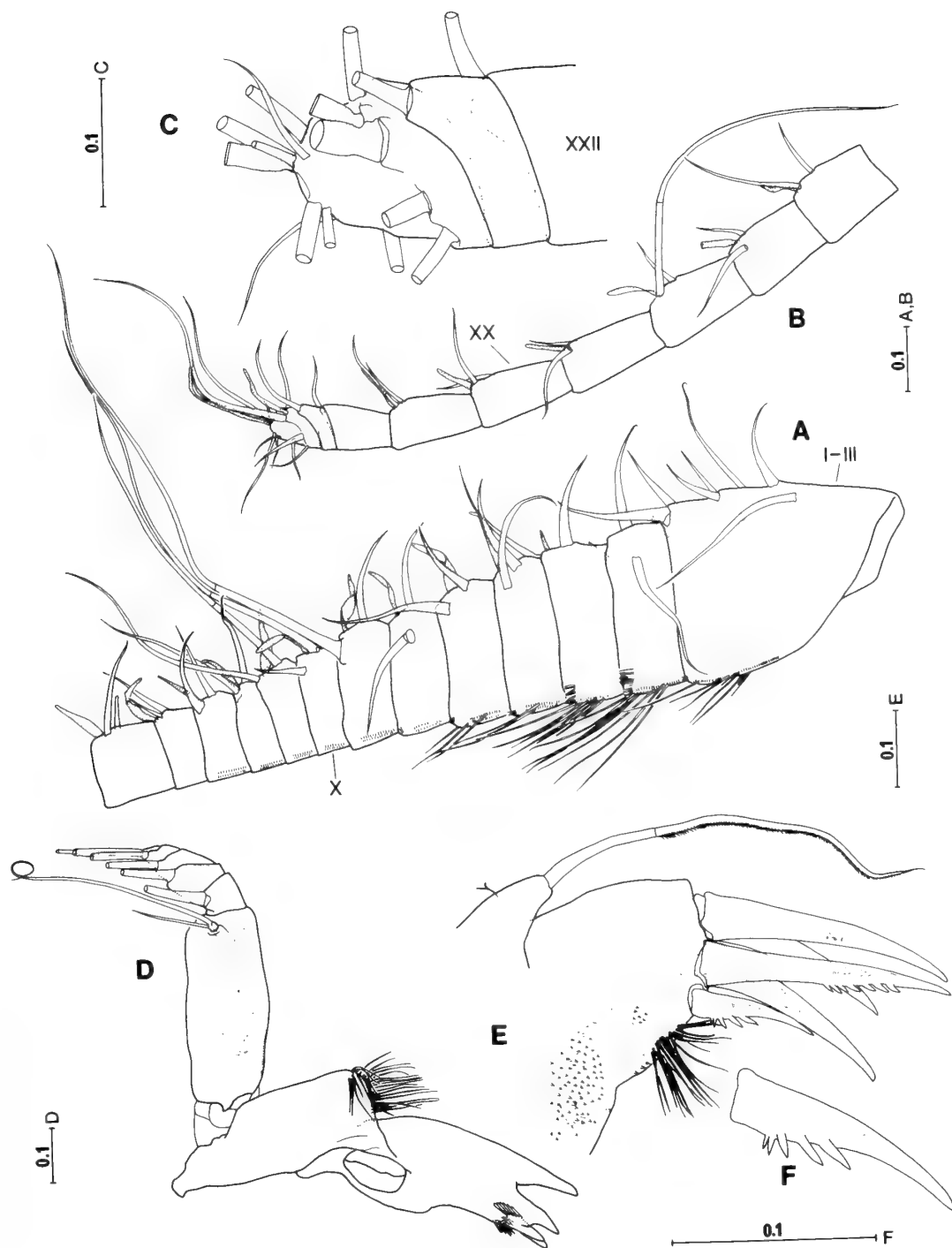


Fig. 4. *Crassarietellus huysi* gen. et sp. nov., female (holotype: E,F; paratype: A-D). A, Antennular segments I to XV; B, Antennular segments XVI to XXVIII; C, Antennular segments XXII to XXVIII; D, Mandible; E, Maxillary praecoxal arthrite and coxal endite; F, Proximal spine on praecoxal arthrite of maxillule. Scales in mm.

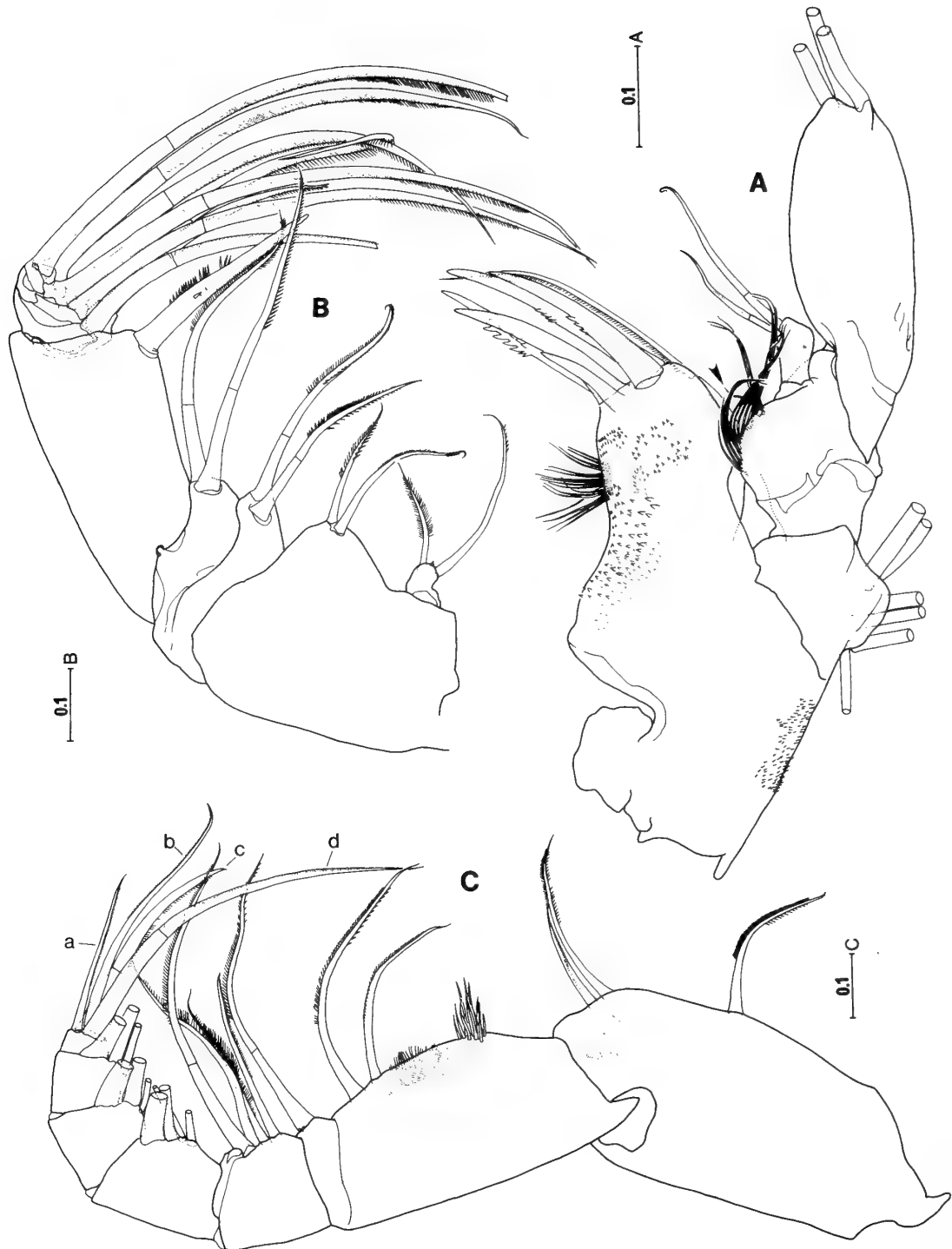


Fig. 5. *Crassarietellus huysi* gen. et sp. nov., female (holotype: C; paratype: A,B). A, Maxillule, with arrowhead indicating enditic seta of basis; B, Maxilla; C, Maxilliped. The armature elements on the sixth endopod segment of maxilliped are identified individually by the letters a to d. Scales in mm.

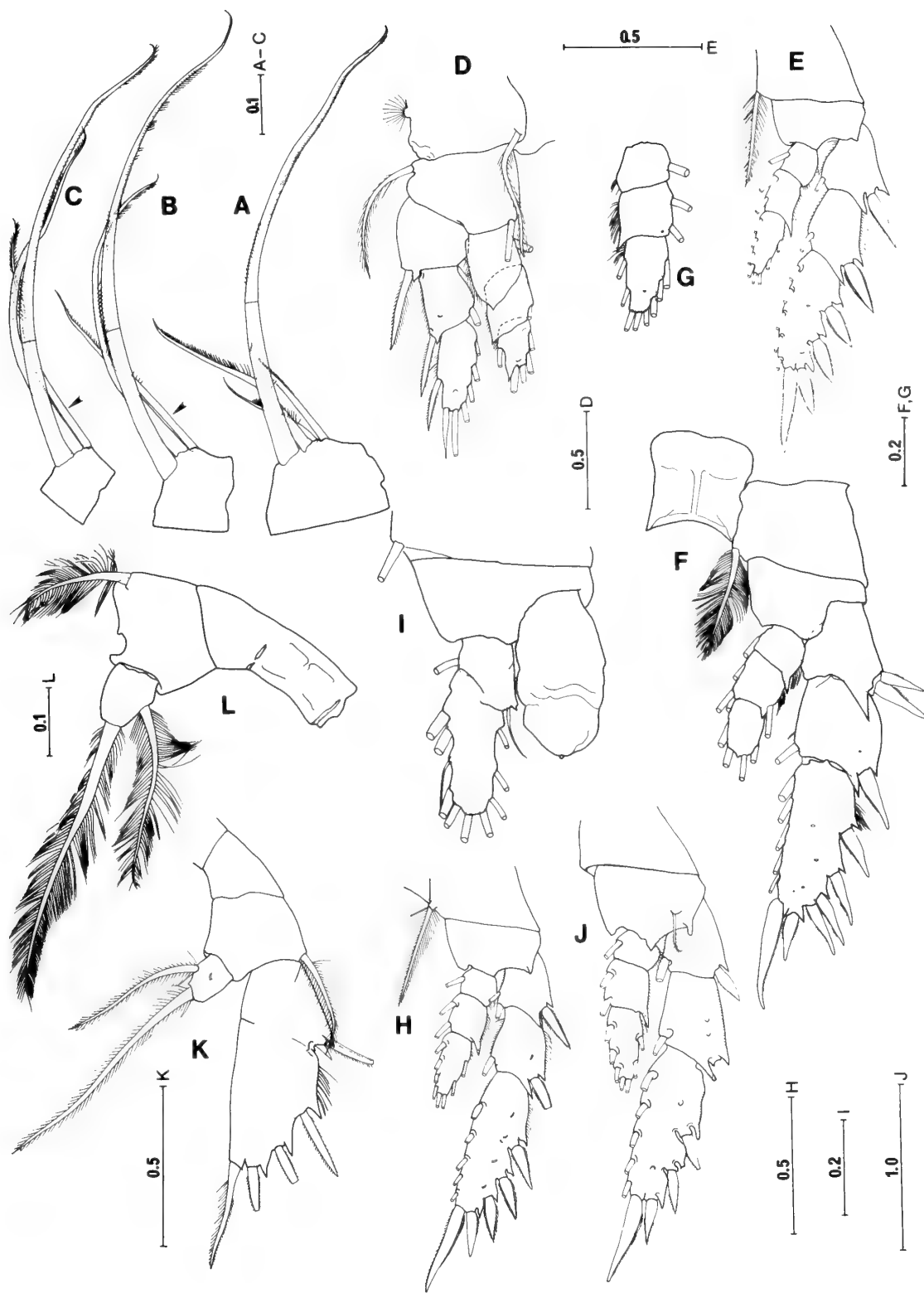


Fig. 6. *Crassarietellus huysi* gen. et sp. nov., female (holotype: A-C,J-L; paratypes: D-I). A, Second endopod segment of maxilliped; B, Third endopod segment of maxilliped, innermost seta indicated by arrowhead; C, Fourth endopod segment of maxilliped, innermost seta indicated by arrowhead; D, Leg 1, anterior surface; E, Leg 2, posterior surface; F, Aberrant leg 3, anterior surface; G, Right endopod of leg 3, anterior surface; H, Another aberrant leg 3, posterior surface; I, Extremely aberrant leg 3, anterior surface; J, Leg 4, posterior surface; K, Left leg 5, anterior surface; L, Right leg 5, anterior surface. Scales in mm.

minute spinules and row of long setules proximally (almost missing in Fig. 4D); endopod rudimentary, 1-segmented, with 2 plumose setae of unequal lengths; exopod 5-segmented, almost completely separate, first to fourth segments each bearing 1 seta, terminal segment with 2 setae, one of which thinner and shorter than other; second segment with patch of minute spinules.

Maxillule (Figs 4E,F,5A): praecoxal arthrite with 5 stout spines, 2 of which (Fig. 4F) bearing 2 rows of strong spinules, and 1 process, patch of long setules, and numerous minute spinules of various sizes along inner margin and patch of fine prominences along outer margin; coxal epipodite with 6 setae; coxal endite with elongate, spinulose seta terminally; basis carrying minute enditic seta and row of long, fine setules along inner margin; endopod rudimentary, 1-segmented, bearing 2 spinulose setae of unequal lengths distally; exopod lamellar, having 3 long, plumose setae distally.

Maxilla (Fig. 5B) stout; first praecoxal endite with 2 spinulose setae and vestigial element; second praecoxal and both coxal endites each carrying 2 spinulose setae; basal endite bearing long, subterminal spine with 2 rows of spinules medially; endopod 4-segmented, first segment with 1 spinulose seta, second to fourth segments having 3, 2 and 2 long, spinulose setae, respectively.

Maxilliped (Figs 5C,6A-C) elongate; syncoxa with 1 medial and 2 subterminal setae and patch of fine spinules subterminally; basis bearing 2 patches of spinules proximally and midway along inner margin and 2 spinulose subterminal setae; endopod 6-segmented, first segment incompletely fused with basis, first to sixth segments carrying 1, 4, 4, 3, 3, and 4 setae, respectively; innermost seta on fourth and fifth segments relatively long; sixth with setae a and b well developed, seta c chitinized, bearing row of simple spinules along inner margin, seta d long, with inner row of simple spinules.

Leg 1 (Fig. 6D); second endopod segment produced at outer angle; third endopod segment produced distally into acute process, with 2 outer lateral spines and terminal plumose seta; first exopod segment produced near outer angle; second and third exopod segments produced at outer angle. Leg 2 (Fig. 6E) and leg 3 (Fig. 6F-I) similar; outer angle of second endopod segment acutely produced; third endopod segment with 4 inner setae. Third legs with several aberrations: extra spine present on each of first (Fig. 6F) and third exopod segments (Fig. 6F,H); extra seta on first (Fig. 6H) and second endopod segments (Fig. 6F); fewer seta on third endopod segment (Fig. 6F); both rami extremely abnormal (Fig. 6I). Leg 4 (Fig. 6J): basis with small plumose seta near base of exopod on posterior surface; terminal endopod segment with 3 inner setae.

Leg 5 (Fig. 6K,L): both legs almost symmetrical; right and left coxae incompletely separate from intercoxal sclerite; basis with relatively narrow base, bearing plumose seta at outer angle; endopod small, 1-segmented, distinctly separate from basis, with inner medial and terminal plumose seta; exopod indistinctly 3-segmented, each almost fused, first and second segment with serrate spine at outer angle, third with 2 terminal and 1 lateral spines.

Male. Unknown.

VARIABILITY. The paratypic females have aberrant third legs (Fig. 6F,H,I). Both paratypes have 4 outer spines on the third exopodal segment of leg 3, but it is likely that the segment normally has 3 outer spines, because the males of *Crassari-*

etellus sp. and other arietellids carry only 3 spines on this segment. An additional spine on the first exopodal segment of leg 3 has also been reported in specimens of some shallow-water hyperbenthic and cave-dwelling species of the calanoid family Pseudocyclopiidae (Scott, 1894; Fosshagen & Iliffe, 1985). Some females of *Paracyclopia naessi* Fosshagen, 1985 had 2 outer spines on the first exopodal segment of leg 3 (Fosshagen & Iliffe, 1985) and this segment of the same leg in *Pseudocyclopia crassicornis* Scott, 1892 was figured with 2 spines (Scott, 1892).

It is interesting to note that it is the same segment of the same leg which carried the extra spine in both *Crassarietellus* and pseudocyclopiids. The presence of a seta on the outer margin of the second endopodal segment of leg 3 (Fig. 6F) is unique for the Calanoida. Elsewhere in the Copepoda such a seta has only ever been found in the two superornatiremid harpacticoids figured by Huys & Boxshall (1991).

REMARKS. The male of *C. huysi* is unknown. *Crassarietellus* sp. described below, which was erroneously considered to be the male of *Sarsarietellus* (= *Scottula*) *abyssalis* (Sars, 1905), is similar to *C. huysi* except in sexual dimorphic characters, but is smaller than *C. huysi*. Considering that the locality of *Crassarietellus* sp. (38°02'N, 10°44'W) is near the type locality of *C. huysi* (20°18.5'N, 21°41.2'W-20°20.8'N, 21°53.0'W), it is possible that this male can be assigned to *C. huysi*.

Crassarietellus sp. (Figs 7-8)

MATERIAL EXAMINED. ♂, Zoological Museum, University of Oslo, Catalog No. F5445-5446, labeled as *Scottula abyssalis* G.O. Sars.

BODY LENGTH. 2.8 mm (after Rose, 1933).

DESCRIPTION. Integument of urosome and appendages pitted as in *Crassarietellus huysi*. Left antennule (Fig. 7A-C) geniculate between ancestral segments XX and XXI, fringed with setules along posterior margins of segments I-X, transverse row of setules on each of segments IV to VIII; fusion pattern and armature as follows: I-IV-9 + 4 aesthetascs, V-2 + aesthetasc, VI-2 + aesthetasc, VII-2 + aesthetasc, VIII-2 + aesthetasc, IX-2 + aesthetasc, X-2 + aesthetasc, XI-2 + aesthetasc, XII-2 + aesthetasc, XIII-2 + aesthetasc, XIV-2 + aesthetasc, XV-2 + aesthetasc, XVI-2 + aesthetasc, XVII-2 + aesthetasc, XVIII-2 + aesthetasc, XIX-1 + aesthetasc + 2 processes, XX-2 + process, XXI-XXIII-1 + aesthetasc + 2 processes, XXIV-XXVIII-12 + 2 aesthetascs; segment XXV incompletely fused with XXVI. Sutures between segment I to IV weakly visible. Right antennule as in female of *Crassarietellus huysi*.

Antenna (Fig. 7D): basis with serrate inner seta; endopod 2-segmented, first segment with short, inner seta at three quarters length and numerous spinules subterminally, second segment with 3 inner setae of unequal lengths and 5 setae terminally, covered almost entirely with spinules; exopod indistinctly 10-segmented, eighth segment fringed with minute spinules along both sides; setal formula of exopod as follows: 0,0,0,1,1,1,1,1,0,3.

Mandibular gnathobase (Fig. 7F) with 3 stout teeth, dorsal-most of which bifid at tip; tuft of long setules present near base of palp. Mandibular palp (Fig. 7E): basis elongate, furnished with numerous minute spinules and row of long setules along inner margin; endopod rudimentary, 1-segmented, bearing 2 unequal setae; seta on first exopod

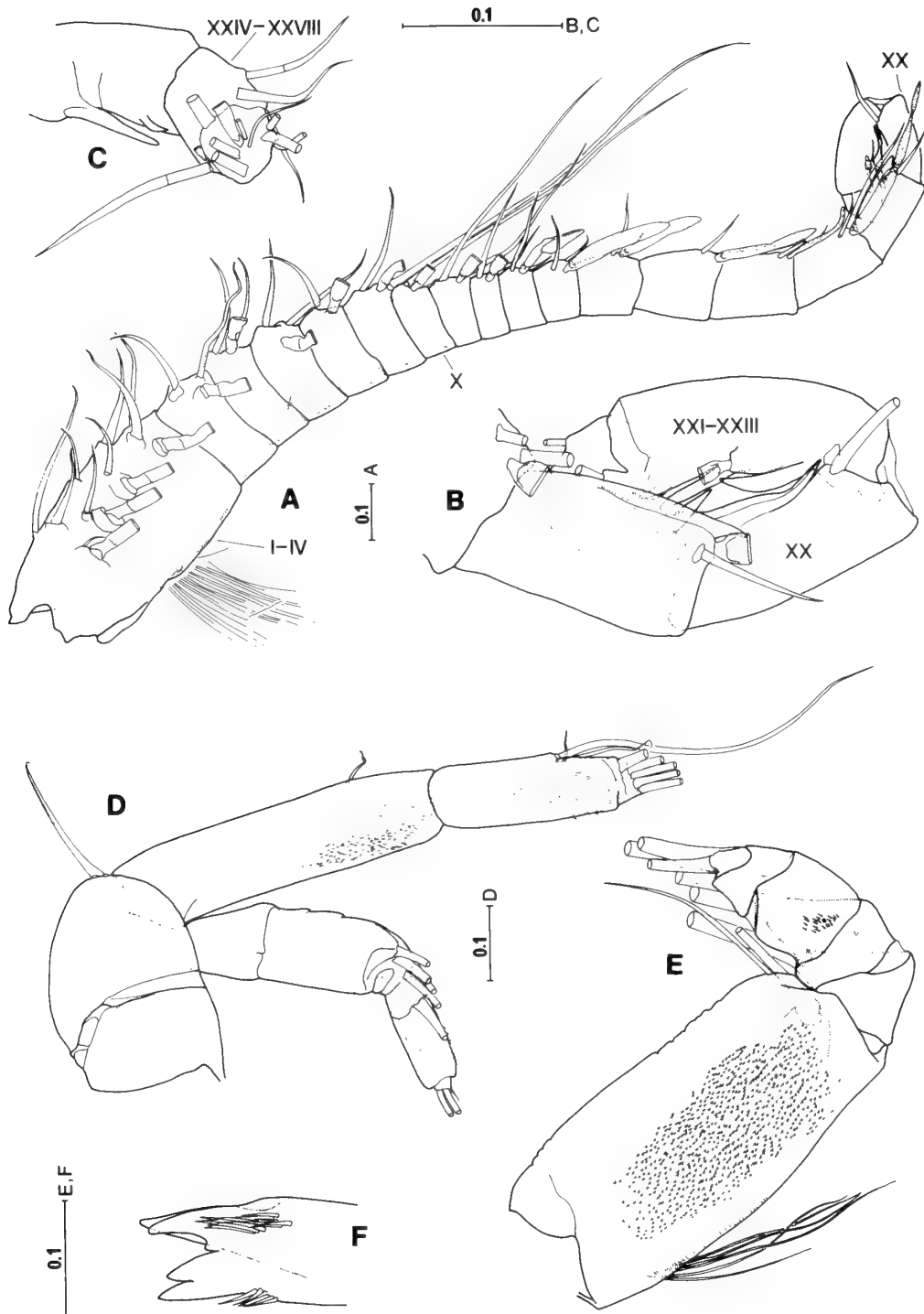


Fig. 7. *Crassarietellus* sp., male. A, Left antennule; B, Antennular segments XIX to XXVIII, elements on segments XXIV-XXVIII omitted except for outer seta; C, Antennular segments XXIV-XXVIII; D, Antenna; E, Mandibular palp; F, Mandibular gnathobasic cutting edge. Scales in mm.

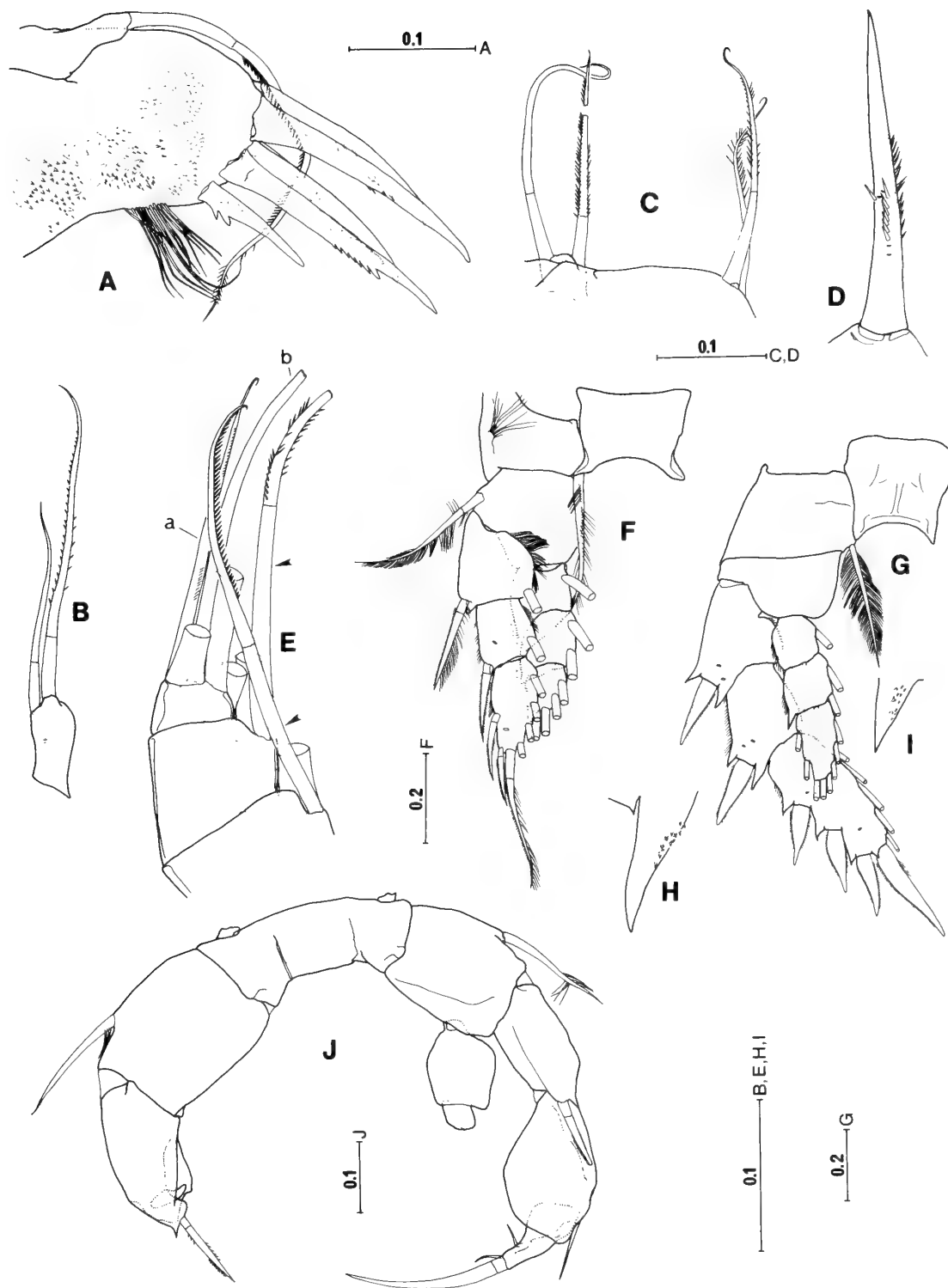


Fig. 8. *Crassarietellus* sp., male. A. Praecoxal arthrite and coxal endite of maxillule; B. Maxillulary endopod; C. First and second praecoxal endites of maxilla; D. Basal spine of maxilla; E. Fourth to sixth endopod segments of maxilliped, inner seta on fourth and fifth segments indicated by arrowhead; F. Leg 1, anterior surface; G. Leg 2, anterior surface; H. Outer distal process on second exopod segment of leg 3; I. Outer process on second endopod segment of leg 3; J. Leg 5, anterior surface, ancestral second and third segments of right exopod missing. Scales in mm.

segment not reduced, fifth segment with 2 developed setae.

Maxillule (Fig. 8A,B): praecoxal arthrite carrying 5 serrate spines and 1 process, with numerous spinules of variable sizes on both sides and patch of setules; coxal endite with long, serrate seta; coxal epipodite bearing 6 setae.

Maxilla: first and second syncoxal endites (Fig. 8C) having 2 setae and vestigial element, and 2 spinulose setae, respectively; basal spine (Fig. 8D) with 3 rows of spinules at midlength.

Maxilliped (Fig. 8E): fourth and fifth endopod segments each with non-reduced innermost seta, sixth segment with setae a and b well developed.

Leg 1 (Fig. 8F): coxa with plumose seta at inner angle and tuft of long setules near outer proximal margin; basis with outer and inner plumose seta; endopod 3-segmented, all segments with outer distal angle produced distally; exopod 3-segmented, first segment with outer setiform spine reaching to distal end of second, third segment with 2 outer lateral spines and 1 spiniform terminal seta. Legs 2 (Fig. 8G) and 3 with the same segmentation and setation; basal inner corner rounded; outer process on second endopod segment (Fig. 8I) with minute spinules along inner margin; terminal outer process on first and second exopod segments (Fig. 8H) also carrying small projections midway along inner margin. Leg 4: coxa unarmed; basis with outer seta on posterior surface; endopod 3-segmented, setal formula 0-1;0-2;2,2,3; exopod distal 2 segments missing, first segment with outer spine and inner seta.

Leg 5 (Fig. 8J): coxae incompletely fused with intercoxal sclerite; basis separate from coxa, bearing outer plumose seta at midlength. Right leg lacking endopod; exopod missing distal segment(s), at least, 2-segmented, first segment with spinulose spine and pointed process at distal angle. Left leg with indistinctly 2-segmented endopod, first segment large, second hemispherical with minute prominence terminally; exopod 3-segmented, first segment with spinulose spine and pointed process on distal corner, second segment expanded, carrying outer spinulose spine at midlength, third segment small, tapering distally, with 1 minute basal element, 2 short medial setae along outer margin and terminal spine as long as second segment.

REMARKS. Since the third leg of *Crassarietellus* sp. has 3 outer spines on the third exopodal segment and 1 inner seta on the first exopodal segment, as most other arietellids, the third legs of the paratypes of *C. huysi* are here interpreted as abnormal.

Genus *Campaneria* gen. nov.

DIAGNOSIS. Only male known. Cephalosome and first pedigerous somite separate. Anal somite almost telescoped into preceding somite; anal operculum not developed. Caudal rami symmetrical, longer than wide, with vestigial seta I, well-developed setae II–VI and minute seta VII.

Left antennule reaching almost to end of urosome, geniculate, 20-segmented; segments II to IV almost fused but sutures clearly visible, segments II and III each bearing seta and aesthetasc; segment XIII with seta, aesthetasc and process representing modified seta; segment XXI separate from XXII; segment XXV incompletely fused with XXVI; segment XIII with seta and process; compound segment XXVI–XXVIII with 8 setae and aesthetasc; segment II

(probably, originally from I) to XIII fringed with setules posteriorly.

Antenna: first endopod segment having inner seta, second segment bearing 3 inner setae subterminally and 5 setae terminally; exopod indistinctly 8-segmented. Mandibular gnathobase with tuft of setules. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long.

Maxillule: praecoxal arthrite carrying 5 spines, 3 of which weakly serrate medially, and process; coxal endite with long seta; coxal epipodite with 6 setae; second basal endite represented by vestigial seta; endopod bulbous, 1-segmented, having 2 setae.

Maxilla: first syncoxal endite with 2 setae and vestigial element; second syncoxal endite with 2 setae; basal endite bearing stout spine with 3 rows of spinules proximally.

Maxilliped: setal formula of endopod 1,4,4,3,3,4; fourth endopod segment with non-reduced innermost seta, fifth segment with shorter innermost seta than fourth, sixth segment with seta a vestigial and seta b relatively long.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 lacking inner coxal seta. Leg 5 with coxae and intercoxal sclerite fused to form a common plate; coxa separate from basis. Right leg: endopod 1-segmented, bulbous; exopod indistinctly 3-segmented, distal 2 segments almost fused, expanded medially, with rounded process medially and 2 setules and 1 prominence terminally. Left leg: endopod indistinctly 2-segmented, unarmed; exopod 2-segmented, distal segment curved outwards near tip, with 3 setae terminally and 1 seta medially.

TYPE SPECIES. *Campaneria latipes* gen. et sp. nov.

REMARKS. As already suggested by Bradford (1969), we conclude that the single paratypic male of *Scutogasterulus pelophilus* belongs to a different species from the female.

Although sexual dimorphism in mouthparts is exhibited in arietellids such as *Arietellus* (present study) and *Paraugaptilus* (Deevey, 1973; present study), the sexual differences are restricted to the antennary rami and the first mandibular exopod segment. However, the male differs from the holotype female of *S. pelophilus* in armature elements on the mouthparts and leg 1 as follows: (1) the female has 'shield-shaped' appendages (= ornamentation) (Bradford, 1969) on terminal setae of the maxilla and maxilliped, while the male lacks such ornamentation; (2) there is single inner seta on the first antennary endopod segment in the male but none in the female; (3) the praecoxal arthrite of maxillule has 6 elements in the male (5 spines and 1 process) and 5 in female (4 spines and 1 process); (4) the maxillary endopod has 2 setae in the male and 1 in the female; (5) the first and second praecoxal endites of the maxilla bear 2 setae plus a vestigial element and 2 setae in the male, and 1 seta plus a vestigial element and 1 seta in the female, respectively; (6) seta b on the sixth endopod segment of maxilliped is long in the male but short in the female; (7) the third exopod segment of leg 1 has 2 outer spines in the male but only 1 in the female. As far as the armature is concerned, the female shows more apomorphic character states than the male. In particular, the magnitude of the differences in the antenna, maxilla, maxilliped and leg 1 is greater than not only variation within a species but also normal interspecific discrepancies between congeners. A new genus is, therefore, established to accommodate the male.

The male of the new genus is similar to that of *Crassarietellus*. However, the left antennule, the antennary exopod, the maxillary praecoxal arthrite, and the fifth and sixth endopod segments of maxilliped are different: (1) left antennule reaching almost to end of urosome in *Campaneria*, but, possibly, at most to end of prosome in *Crassarietellus*; (2) antennular segments II to IV partly fused in *Campaneria*, but almost completely so in *Crassarietellus*; (3) antennular segments II and III each bearing single seta and aesthetasc in *Campaneria*, but 2 setae and aesthetasc in *Crassarietellus*; (4) antennular segments XXI and XXII completely separate in *Campaneria*, but almost fully fused in *Crassarietellus*; (5) seta on antennular segment XV modified into process in *Crassarietellus*, but not in *Campaneria*; (6) antennary exopod indistinctly 8-segmented in *Campaneria* but 10-segmented in *Crassarietellus*; (7) spines on maxillary praecoxal arthrite finely serrate in *Campaneria*, but strongly serrate in *Crassarietellus*; (8) innermost seta on the fifth endopod segment of maxilliped relatively short in *Campaneria*, but long in *Crassarietellus*; (9) seta a on the sixth endopod segment of maxilliped relatively reduced in *Campaneria*, but not in *Crassarietellus*.

The leg 5 of *Campaneria* is also similar to that of *Crassarietellus* sp., particularly in having a 2-segmented left endopod, but can be distinguished by the presence of the right endopod and by the 2-segmented left exopod.

ETYMOLOGY. The new genus *Campaneria* is named in honour of the late Dr. A. Campaner who was the first to be interested in the phylogenetic relationships between arietellid genera (gender feminine). The specific name *latipes* (Latin *latus* meaning broad; Latin *pes* meaning leg) refers to the broad compound exopod segments of the right leg 5 of the male.

ECOLOGICAL NOTE. *Campaneria* was collected by a trawl from the near-bottom samples taken at depths of 1234–1260 m off northeastern New Zealand (Bradford, 1969). Since the genus has never been captured in plankton hauls, it is most likely hyperbenthic.

Campaneria latipes gen. et sp. nov. (Figs 9–10)

MATERIAL EXAMINED. ♂, New Zealand Oceanographic Institute Reg. No. 121, labelled as *Scutogerulus pelophilus* (♂).

BODY LENGTH. 3.9 mm (after Bradford, 1969).

DESCRIPTION. Anal somite (Fig. 9A) small, almost telescoped into preceding somite; caudal rami (Fig. 9A) symmetrical, seta I vestigial, setae II–VI developed, seta VII minute.

Left antennule (Fig. 9B–F): segment I damaged, but with 3 setae and aesthetasc (only this segment still remained on the body); segments II and III fused with suture visible anteriorly; segments III and IV, and XXIV–XXV and XXVI–XXVIII incompletely fused. Fusion pattern and armature elements as follows: II–IV–4 + 3 aesthetascs, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–1 + aesthetasc + process, XI–2 + aesthetasc, XII–1 + aesthetasc + process, XIII–1 + aesthetasc + process, XIV–1 + aesthetasc + process, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–1 + aesthetasc + 2 processes, XX–1 + aesthetasc + process, XXI–aesthetasc + 2 processes,

XXII–XXIII–1 + process (XXII-process, XXIII–1), XXIV–XXVIII–12 + 2 aesthetascs.

Antenna: inner basal seta present; endopod (Fig. 9G) 2-segmented, first segment with short inner seta, second segment with 3 inner setae of unequal lengths subterminally and 5 setae terminally; exopod (Fig. 10A) indistinctly 8-segmented, second segment elongate, setal formula 0,1,1,1,1,1,0,3.

Mandibular palp (Fig. 10E): endopod rudimentary, 1-segmented, carrying 2 setae of unequal lengths; first exopod segment bearing non-reduced seta, fifth segment with 1 long and 1 shorter seta.

Maxillule: praecoxal arthrite (Fig. 10B) bearing 5 spines and 1 process, 3 of which serrate medially, with row of long setules and patch of minute spinules proximally; coxal endite (Fig. 10C) with long spinulose seta terminally; coxal epipodite with 6 setae; minute endite seta present on basis (Fig. 10D), endopod bulbous, 1-segmented, with 2 spinulose setae of unequal lengths.

Maxilla: first praecoxal endite with 2 spinulose setae and vestigial element, second endite with 2 bipinnate setae (Fig. 10F); basal spine (Fig. 10G) with 3 rows of spinules of different sizes proximally.

Maxilliped: fourth and fifth endopod segments (Fig. 10H) each having non-reduced, spinulose innermost seta, but seta on fourth segment much longer than on fifth; sixth endopod segment (Fig. 10I) with medium-length seta b and vestigial seta a.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 having outer basal seta, but lacking inner coxal seta.

Leg 5 (Fig. 10J): coxae and intercoxal sclerite almost fused, but suture visible on posterior surface; basis separate from coxa. Right leg: basal seta missing; endopod 1-segmented, with tuft of short setules terminally; exopod indistinctly 3-segmented, first triangular, carrying spine at outer angle, distal 2 segments almost fused, but suture visible on both surfaces, expanded medially, having outer seta proximally, round inner process with 3 minute prominences at tip medially, and 2 setae and 1 prominence along outer terminal margin. Left leg: basal seta missing; endopod indistinctly 2-segmented, unarmed; exopod 2-segmented, first segment triangular, bearing spine on outer corner, second segment expanded inwards, curved outwards at about three quarters length, with fine medial seta and 3 terminal setae of unequal lengths.

REMARKS. In her original description Bradford (1969) overlooked the antennary basal seta, the inner seta on the first antennary endopod segment, 3 short setae on the distal 2 endopod segments of the maxilliped, the outer basal seta of leg 4, and the fine midlength seta on the second exopod segment of left leg 5.

Genus Paraugaptiloides gen. nov.

DIAGNOSIS. Only male known. Body similar to that of *Paraugaptilus*; cephalosome separate from first pedigerous somite; prosome rounded anteriorly and produced posteriorly, with small dorsolateral prominence and bluntly produced lateral lobe on each side; lateral flap of cephalosome developed to cover bases of mouthparts. Caudal rami symmetrical with setae II and III normally developed.

Male left antennule 19-segmented, fringed with setules along posterior margin of first segment only; segments I and

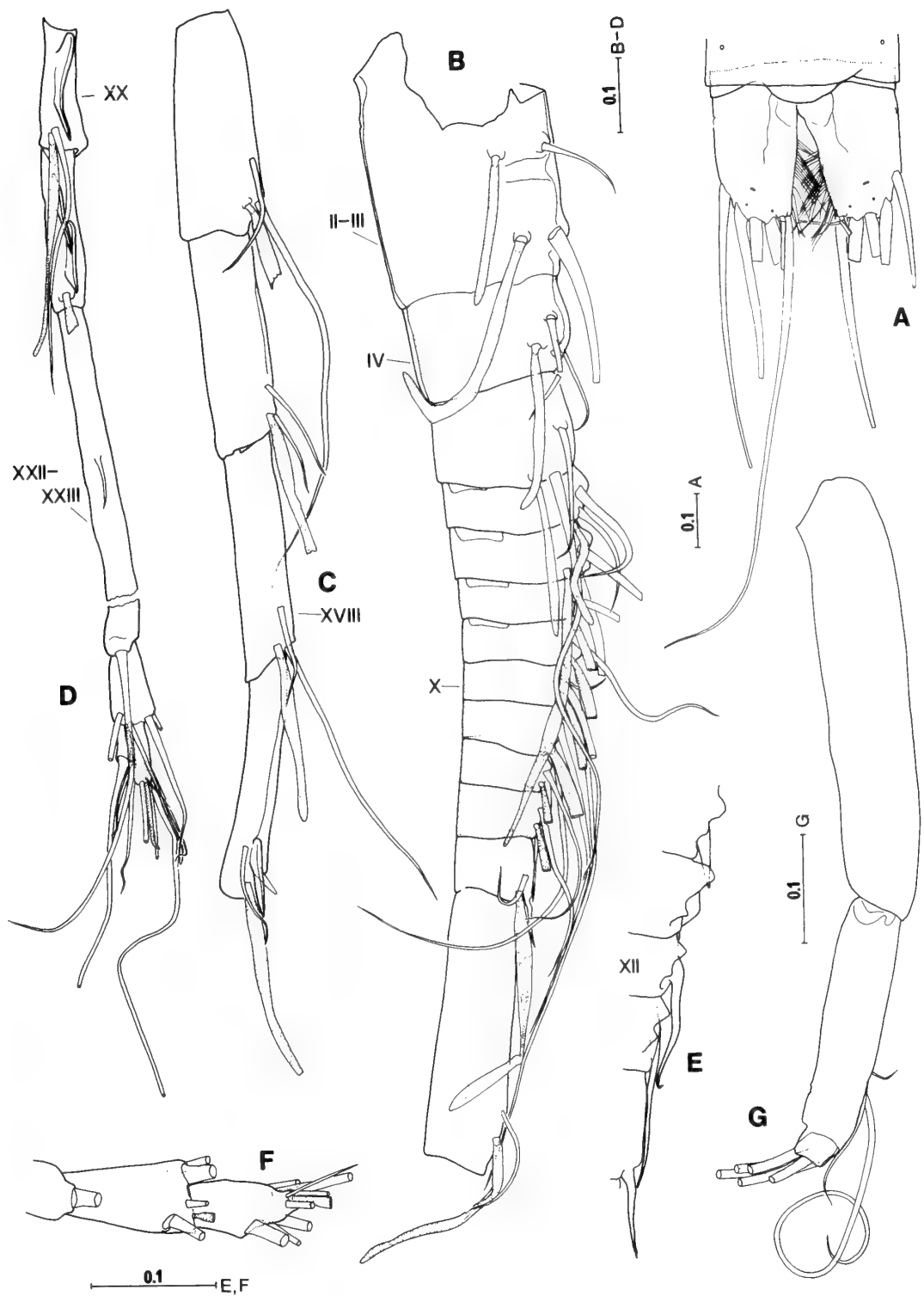


Fig. 9. *Campaneria latipes* gen. et sp. nov., male (holotype). A, Anal somite and caudal rami, dorsal view; B, Left antennular segments II to XV; C, Left antennular segments XVI to XIX; D, Left antennular segments XX to XXVIII; E, Anterior processes on segments XX-XXIV of left antennule; F, Left antennular segments XXIV to XXVIII; G, Antennary endopod. Scales in mm.

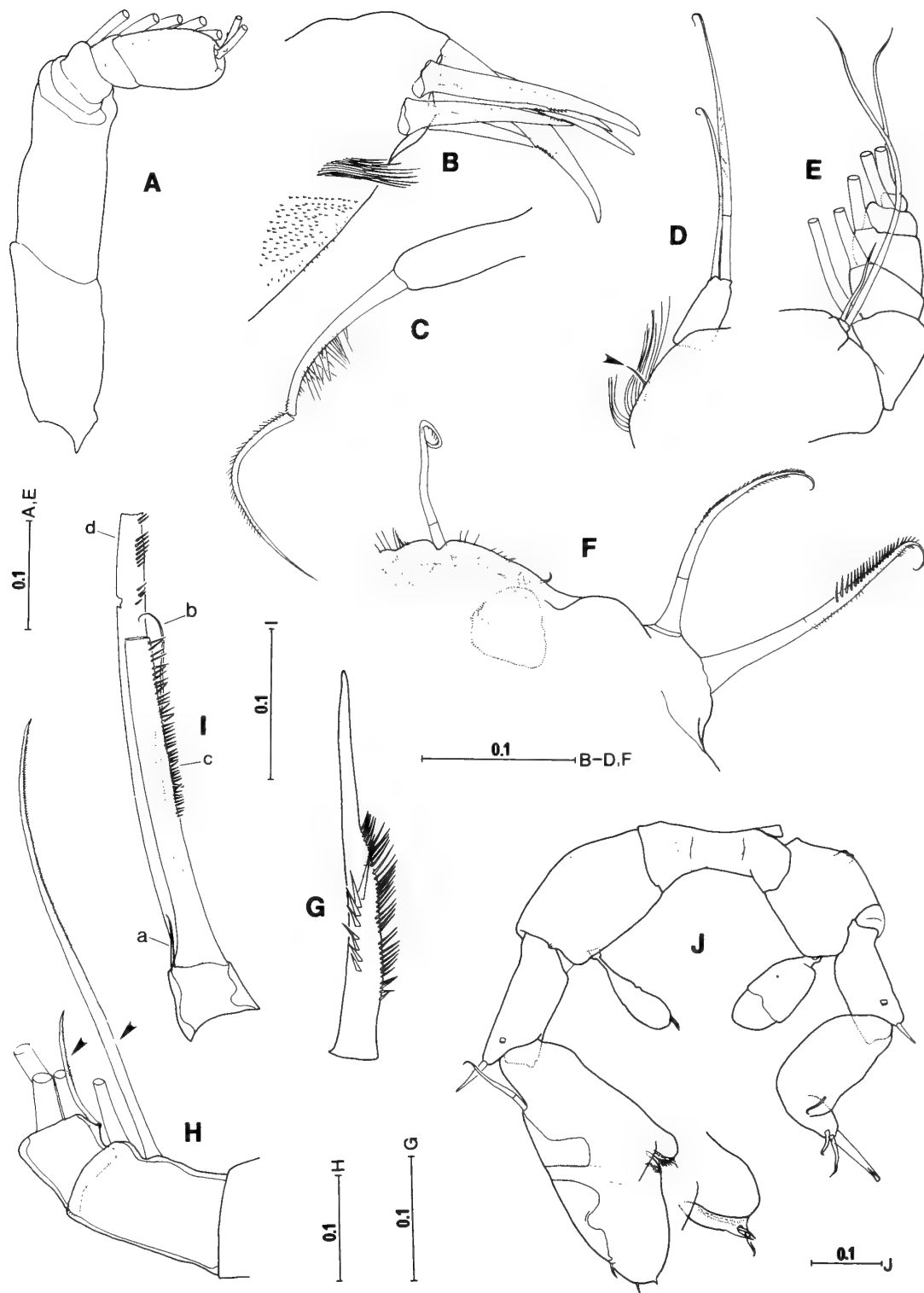


Fig. 10. *Campaneria latipes* gen. et sp. nov., male (holotype). A, Antennary exopod; B, Praecoxal arthrite of maxillule; C, Coxal endite of maxillule; D, Maxillulary endopod with basal seta indicated by arrowhead; E, Mandibular endopod and exopod; F, First and second praecoxal endite of maxilla; G, Basal spine of maxilla; H, Fourth and fifth endopod segments of maxilliped, innermost seta indicated by arrowhead; I, Sixth endopod segment of maxilliped; J, Leg 5, anterior surface. Scales in mm.

II each with 1 seta; segment XIII with seta and process; segment XXI fused with XXII; compound segment XXIV–XXV with large cuticular process; compound segment XXVI–XXVIII with 8 setae and aesthetasc. Antenna: first endopod segment without inner seta, second segment with 2 inner setae at midlength and 5 setae and 1 setule terminally; exopod indistinctly 8-segmented, setal formula 0,1,1,1,1,0,3. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long.

Maxillule: praecoxal arthrite with 5 spines and 1 process; coxal endite carrying long seta; coxal epipodite bearing 8 setae; no basal seta; endopod 1-segmented, bearing 2 setae. Maxilla: first praecoxal endite with 2 setae and 1 vestigial element; second praecoxal endite with 2 setae; basal spine with 2 rows of spinules. Maxilliped: endopodal setal formula 1,4,4,3,3,4; innermost seta on fourth and fifth endopod segments not vestigial; seta a on sixth endopod segment reduced, seta b relatively long.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 with vestigial element on inner distal corner of coxa. Leg 5: coxae fused with intercoxal sclerite; basis and coxa separate in left leg and incompletely fused in right. Right leg: endopod 1-segmented, rudimentary, unarmed; second exopod segment expanded inwards, almost completely separate from third segment, third segment triangular, tapering distally, with 1 minute outer and 1 terminal setules. Left leg: endopod 2-segmented, unarmed; exopod 3-segmented, distal 2 segments completely separate, second segment expanded inwards, third segment with 2 long stout processes directed laterally.

TYPE SPECIES. *Paraugaptilus magnus* Bradford, 1974 (monotypic).

REMARKS. Bradford (1974) assigned a male collected from a depth of 1697 m off the north-east coast of North Island, New Zealand, to the genus *Paraugaptilus*, although she mentioned seven distinct characters of the species that would possibly necessitate its removal to a new genus. Morphological discontinuities can be found between *P. magnus* and other species of *Paraugaptilus* as follows: (1) left antennular compound segment XXVI–XXVIII with 8 setae and aesthetasc; (2) antennary exopod indistinctly 8-segmented, with setal formula 0,1,1,1,1,0,3; (3) mandibular endopod almost fused with basis, but represented by a rudimentary segment with 2 setae; (4) maxillule with long seta on coxal endite, 1 basal seta and 2 setae on 1-segmented endopod; (5) maxilla with 2 setae and 1 vestigial element on first praecoxal endite and 2 setae on second; (6) setae on maxillary endopod ornamented with row of simple spinules along inner margin but lacking triangular-shaped ornamentation found in other species of *Paraugaptilus*; (7) seta b on sixth endopod segment of maxilliped not reduced; (8) second and third exopod segments of right leg 5 almost completely separate; (9) leg 5 with 2-segmented left endopod.

In genera accommodating several species, such as *Paramisophria*, *Arietellus* and *Metacalanus*, the praecoxal arthrite, coxal endite and endopod of maxillule, first praecoxal endite of maxilla, and leg 5 exhibit wide interspecific variation in armature. However, the armature of the antennary exopod, mandibular palp, second praecoxal endite of maxilla, endopods of male leg 5 are relatively consistent within each genus. In particular, the significant differences found in the anten-

nary exopod, the mandibular endopod and the second praecoxal endite of the maxilla support the proposal to assign *P. magnus* to a new genus, *Paraugaptiloides*.

The new genus is similar to *Arietellus* and *Paramisophria* in the segmentation and setation of appendages, but can be distinguished from these genera by: (1) the presence of a large cuticular process on left antennular segments XXIV–XXV (shared with *Paraugaptilus*); (2) the lack of a seta on the first endopod segment of antenna, also absent in *Arietellus* but present in *Paramisophria*; (3) the 2 inner medial setae on the second endopodal segment of antenna in *Paraugaptiloides* and *Arietellus*, compared to 3 in *Paramisophria*; (4) outer seta on fifth exopodal segment of mandible relatively long in *Paraugaptiloides* and *Paramisophria*, but vestigial in *Arietellus*; (5) mandibular endopod 1-segmented with 2 setae in *Paraugaptiloides* and *Paramisophria*, but absent in *Arietellus*; (6) maxillule with 1 basal and 2 endopodal setae in *Paraugaptiloides* and *Paramisophria*, but no basal and, at most, single endopodal seta in *Arietellus*; (7) maxillary basal spine ornamented with spinules in *Paraugaptiloides* and *Arietellus*, but no ornamentation in *Paramisophria*; (8) innermost seta on fourth and fifth endopodal segments of maxilliped vestigial in *Arietellus*, but not in *Paraugaptiloides* and *Paramisophria*; (9) seta a on the sixth endopodal segment of maxilliped reduced only in *Paraugaptiloides* and *Arietellus*; (10) the presence of vestigial element on inner distal angle of coxa of leg 4 (shared with *Paraugaptilus*); (11) left leg 5 endopod 2-segmented in *Paraugaptiloides* and *Arietellus*, but 1-segmented in *Paramisophria*; (12) right endopod of leg 5 present in *Paraugaptiloides* and *Arietellus*, but absent in *Paramisophria*.

ETYMOLOGY. The name refers to the close relationship of the new genus to *Paraugaptilus*.

ECOLOGICAL NOTE. The male of *P. magnus* was first collected from 1697 m depth off New Zealand (Bradford, 1974), and has been reported recently from the near-bottom (1060–1070 m depths) in the southwestern Indian Ocean (Heinrich, 1993). It is likely that *P. magnus* is widely distributed in deep waters of the Indo-Pacific region. Although the species was collected from the near-bottom in the Indian Ocean (Heinrich, 1993), the well-developed antennules suggest a relatively loose association with the bottom (Campaner, 1984).

Paraugaptiloides magnus, new combination (Figs 11–12)

MATERIAL EXAMINED. ♂, holotype, New Zealand Oceanographic Institute H-199.

BODY LENGTH. 4.85 mm (after Bradford, 1974).

DESCRIPTION. Cephalosome separate from first pedigerous somite. Caudal ramus with setae II–VI well developed.

Left antennule (Fig. 11A,B) 19-segmented, the fusion pattern and armature elements almost same as in *Paraugaptilus*, except for those of segments XXIV to XXVIII: segment XXIV–XXV with large anterior process reaching well beyond antennular tip (Fig. 11B). Right antennule: segments I to X fringed with long setules along posterior margin; segments X and XI, and XIV and XV only partly fused; segment XXIII and XXIV almost separate; segments XXV and XXVI almost fused with suture visible; fusion pattern and armature elements as follows: I–III–7 + 3 aesthetascs, IV–2 (element

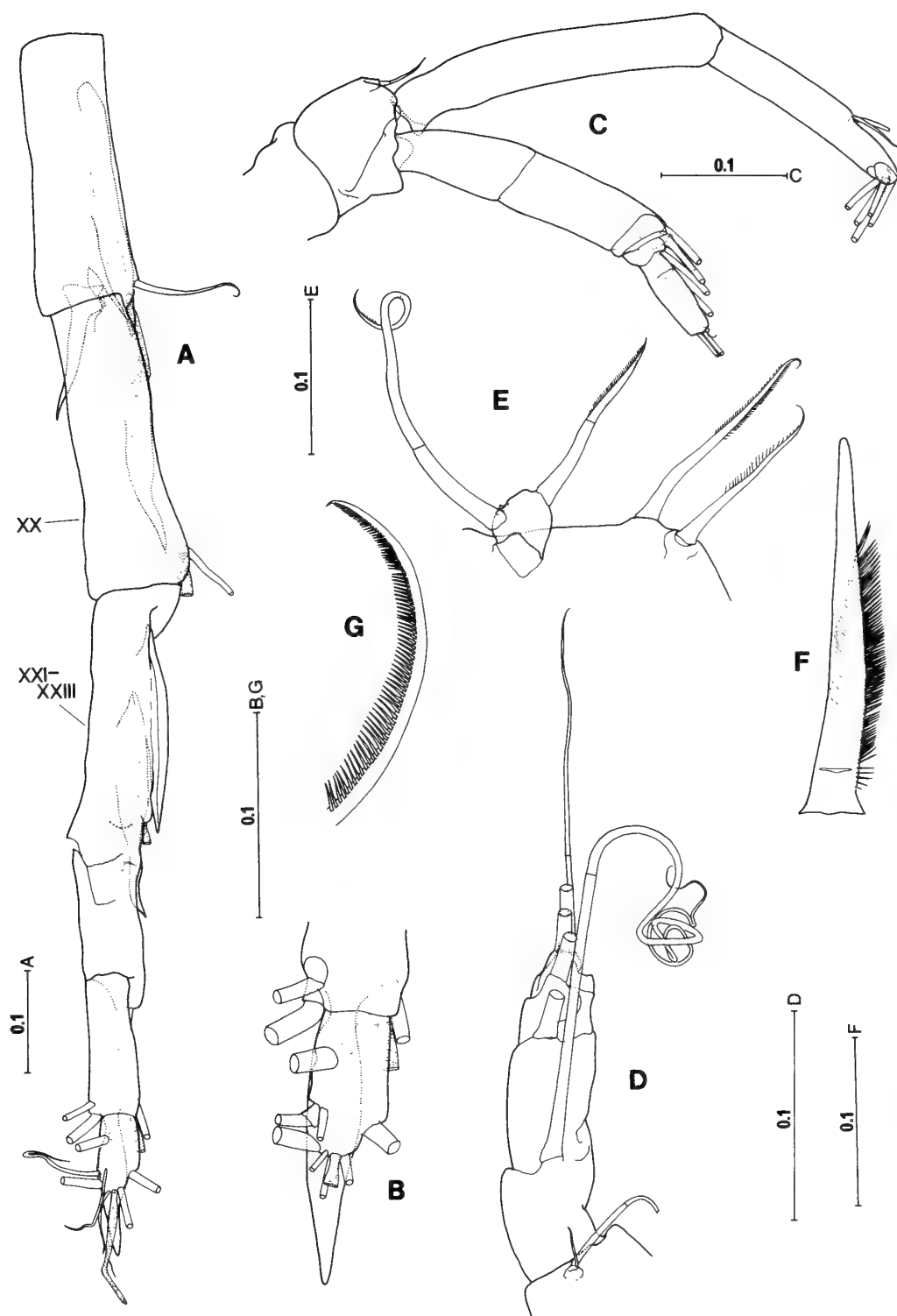


Fig. 11. *Paraugaptiloides magnus* gen. et sp. nov., male (holotype). A, Left antennular segments XIX to XXVIII; B, Left antennular segments XXVI to XXVIII; C, Antenna; D, Mandibular endopod and exopod; E, First and second praecoxal endites of maxilla; F, Basal spine of maxilla; G, Terminal seta on fourth endopod segment of maxilla. Scales in mm.

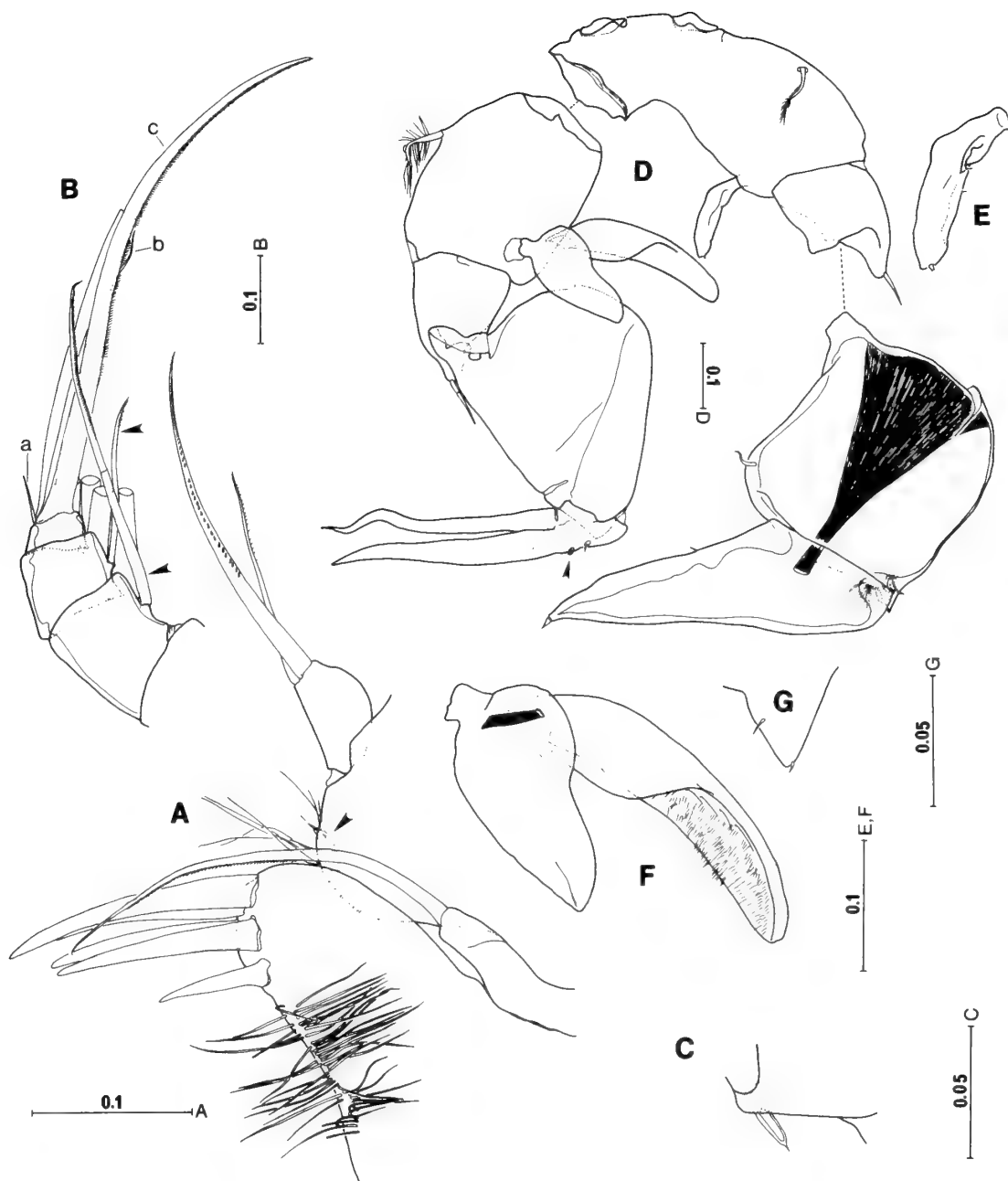


Fig. 12. *Paraugaptiloides magnus* gen. et sp. nov., male (holotype). A, Praecoxal arthrite, coxal endite, basal endite and endopod of maxillule, basal seta indicated by arrowhead; B, Fourth to sixth endopod segments of maxilliped, innermost seta on fourth and fifth segments indicated by arrowhead; C, Inner coxal seta of leg 4; D, Leg 5, posterior surface, scar of element on third exopod segment of left leg indicated by arrowhead; E, Right endopod of leg 5; F, Left endopod of leg 5; G, Inner distal process on second exopod segment of right leg 5. Scales in mm.

missing), V-1 + aesthetasc (element missing), VI-2 + aesthetasc, VII-2 + aesthetasc, VIII-2 + aesthetasc, IX-2 + aesthetasc, X-1 + aesthetasc + process, XI-2 + aesthetasc, XII-2 + aesthetasc, XIII-2 + aesthetasc, XIV-1 + aesthetasc + process, XV-2 + aesthetasc, XVI-2 + aesthetasc, XVII-2 + aesthetasc, XVIII-2 + aesthetasc, XIX-2 + aesthetasc, XX-1 + aesthetasc (element missing), XXI-2 + aesthetasc, XXII-1, XXIII-1, XXIV-XXVIII-12 + 2 aesthetascs (XXIV-2, XXV-2 + aesthetasc, XXVI-XXVIII-8 + aesthetasc).

Antenna (Fig. 11C): first endopod segment lacking inner seta, second segment with 2 inner setae of unequal lengths subterminally and 5 setae and 1 setule terminally; exopod indistinctly 8-segmented, setal formula 0,1,1,1,1,1,0,3.

Mandible: gnathobase with 3 cusped teeth, dorsalmost of which bifid at tip; the medial part of gnathobase is damaged and it is not known whether or not a tuft of setules is present. Mandibular endopod (Fig. 11D) rudimentary, 1-segmented, almost fused with basis, carrying 2 setae of unequal lengths; first exopod segment with well developed seta, fifth segment

with non-reduced outer seta (Fig. 11D).

Maxillule (Fig. 12A): praecoxal arthrite with 5 bare spines and 1 shorter process; coxal epipodite with 8 setae; coxal endite with long, spinulose seta; vestigial basal seta present (indicated by arrowhead); endopod bulbous, 1-segmented, bearing 2 relatively long, spinulose setae terminally.

Maxilla: first praecoxal endite with 2 setae and 1 vestigial element, second with 2 spinulose setae; basal spine (Fig. 11F) with 2 rows of spinules; setae on endopod well developed, ornamented with row of long, simple spinules along inner margin (Fig. 11G). Maxilliped (Fig. 12B): innermost seta on fourth and fifth endopod segments (indicated by arrowhead) not reduced; seta a on sixth endopod segment reduced; seta b relatively long; setae c and d simply ornamented with spinules along inner margin.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 with vestigial element on inner distal angle of coxa (Fig. 12C). Leg 5 (Fig. 12D-G): coxae and intercoxal sclerite completely fused to form common base; coxa and basis incompletely fused in right leg and separate in left. Right leg: endopod (Fig. 12E) 1-segmented, spatulate, with minute sensillum on outer proximal margin and tubular prominences terminally; first exopod segment produced on outer angle, with minute spine, second segment almost completely separate from third, with 2 tufts of fine setules at inner distal angle, minute sensillum at midlength of inner distal triangular process (Fig. 12G) and outer terminal spiniform seta, third segment triangular, tapering distally, with minute sensillum at outer middle margin and short vestigial element terminally; third segment with well developed muscles proximally. Left leg: endopod (Fig. 12F) distinctly 2-segmented, first segment produced terminally, second separate from first, spatulate, covered by numerous fine setules on outer surface, with attachment of muscles proximally; first exopod segment similar to that of right leg, second expanded inwards with outer seta subterminally, third segment small, separate from second, with 2 elongate, chitinized processes terminally and minute setule and scar of outer element proximally.

REMARKS. The fifth leg of the new genus exhibits a more primitive state than *Paraugaptilus* in: (1) 2-segmented left endopod; (2) both exopods 3-segmented. The right third exopodal segment of *Paraugaptiloides* is certainly movable with well-developed muscles originating in the preceding segment, while the counterpart of *Paraugaptilus* is almost fused with the preceding segment and has reduced musculature (see Figs 30F, 32H). It is probably not movable. In addition, the second segment of the left endopod in *Paraugaptiloides* is likely to be movable as indicated by the presence of a muscle extending between first and second segments.

Genus Arietellus Giesbrecht, 1892

DIAGNOSIS (emended). Female. Body relatively large, measuring approximately 3 to 7 mm in total length. Prosome pointed or rounded frontally; cephalosome separate from first pedigerous somite; last prosomal somite with pair of blunt dorsolateral processes and paired ventrolateral processes, symmetrical or asymmetrical, strongly or weakly produced backwards. Genital double-somite longer than wide, with pair of gonopores ventrolaterally and copulatory pore ventromedially; seminal receptacle relatively large, bulbous, located laterally. Anal somite large; anal operculum not developed. Caudal rami symmetrical, longer than wide,

divergent or not, with well developed setae II to VII.

Antennule symmetrical, distinctly 20-segmented; posterior margin fringed with long setules from segment I to X; segments I to IV and XXIII to XXVIII fused; segments IV, VI and XII without aesthetasc; compound segment XXVI-XXVIII with 7 setae and aesthetasc. Antenna: first endopod segment unarmed; second segment with 2 inner setae, reduced in some species, and 5 setae and setule terminally; exopod indistinctly 7- or 8-segmented, segment VIII unarmed. Mandibular gnathobase lacking tuft of setules at midlength; 3 cusped teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: endopod absent; first exopod segment with reduced or normal seta, outer seta on fifth segment vestigial. Maxillule: praecoxal arthrite with 6 elements (5 spines and 1 process); coxal endite bearing 1 relatively short, thick seta, fringed with long setules; coxal epipodite with 8 setae; outer basal seta absent; endopod rudimentary, almost fused to basis or 1-segmented, bulbous, with 1 seta terminally. Maxilla: first and second praecoxal endites carrying 1 and 2 setae, respectively; basal spine with 2 rows of spinules; endopod setae armed with stout spinules fringed with lamellar structure basally. Maxilliped: setal formula of endopod segments of maxilliped: 1,4,4,3 or 2,3 or 2,4 (innermost seta on fourth and fifth segments reduced or completely lacking in some species); setae a and b on sixth segment vestigial.

First and third exopod segments of leg 1 bearing 1 and 2 outer spines respectively. Leg 5 reduced; coxae and intercoxal sclerite fused to form common transverse plate; basis and coxa separate or fused; right basal seta longer than left; endopod fused with basis, represented by small knob bearing 1 to 3 setae terminally, vestigial in some species; exopod 1-segmented, bulbous, carrying 1 terminal spine or almost fused to basis, unarmed.

Male. Body as in female, about 4 to 6 mm in total length.

Left antennule 19-segmented, geniculate; segment XXI fused with XXII; segments II and III with 1 seta; segment XIII with seta; segments I to IX fringed with row of long setules along posterior margin.

Second endopod segment of antenna with 1 long and 1 short seta medially; first exopod segment of mandible with normally developed seta.

Leg 5: coxae and intercoxal sclerite fused to form common plate; right coxa and basis incompletely fused; right basal seta remarkably or normally elongate. Right leg: endopod 1-segmented, unarmed; exopod indistinctly 3-segmented, distal 2 segments incompletely fused, second segment with stout process on inner angle, third segment spatulate, with 0-2 vestigial elements. Left leg: endopod indistinctly 2-segmented or 1-segmented, unarmed; exopod 3-segmented, second segment expanded medially, third segment incompletely fused with preceding one, bearing 2 terminal spines, with or without outer minute spinule.

TYPE SPECIES. *Arietellus setosus* Giesbrecht, 1892 (monotypic).

OTHER SPECIES. *A. aculeatus* (T. Scott, 1894); *A. giesbrechti* Sars, 1905; *A. pavoninus* Sars, 1905; *A. plumifer* Sars, 1905; *A. simplex* Sars, 1905 (= *A. major* Esterly, 1906); *A. armatus* Wolfenden, 1911; *A. minor* Wolfenden, 1911; *A. pacificus* Esterly, 1913; *A. tripartitus* C.B. Wilson, 1950; *A. sp.* Bradford, 1974; *A. mohri* (Björnberg, 1975), new combination; *A. sp.* briefly described here.

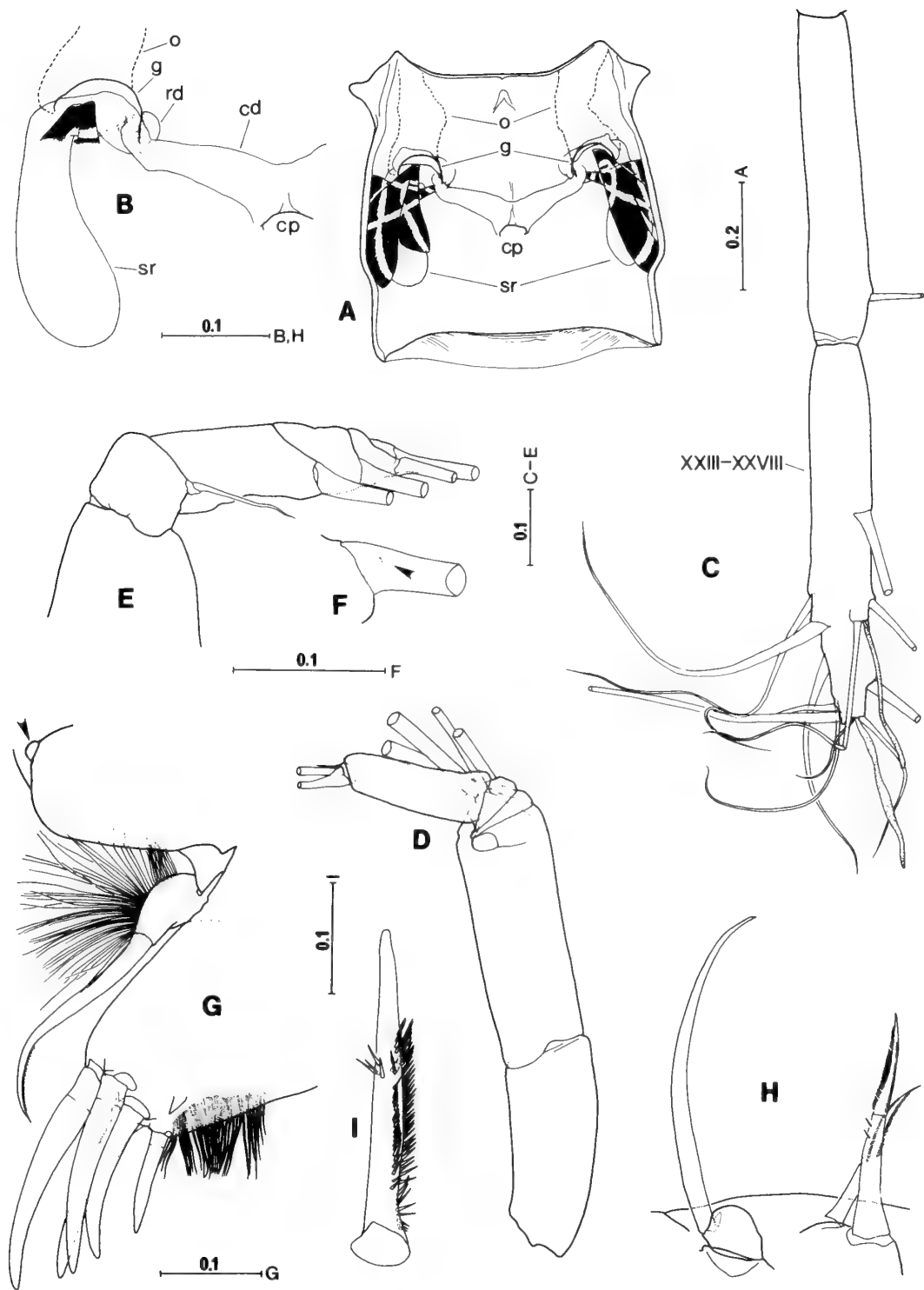


Fig. 13. *Arietellus plumifer*, female. A, Genital double-somite, ventral view; B, Internal structure of right genital system; C, Antennary segments XXII to XXVIII; D, Antennary exopod; E, Mandibular exopod; F, Fifth segment of mandibular exopod, note reduced seta indicated by arrowhead; G, Praecoxal arthrite, coxal endite and endopod of maxillule, rudimentary endopod indicated by arrowhead; H, First and second praecoxal endites of maxilla; I, Basal spine of maxilla. Scales in mm.

REMARKS. The present study revealed that *Paraugaptilus mohri* Björnberg, 1975 belongs to the genus *Arietellus* (see below). *Arietellus* shows sexual dimorphism in the antenna and mandibular palp, as described in *Paraugaptilus* by Deevey (1973). However, no sexual dimorphism is exhibited in the maxillule, the maxilla and the maxilliped.

ECOLOGICAL NOTE. Species of the genus are pelagic and distributed in deep water throughout the world's oceans (Brodsky, 1950; Vervoort, 1965; Roe, 1972, unpublished data; Campaner, 1984).

Arietellus plumifer Sars, 1905 (Figs 13–15, 17A, 18L)

MATERIAL EXAMINED. 2 ♀ and ♂.

BODY LENGTH. ♀ 5.88 mm (28 VI 1985), 6.24 mm (26 XI 1965); ♂ 5.46 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Figs 13A,B, 14) as long as wide, almost symmetrical, with pair of gonopores ventrolaterally and anterior to single ventromedial copulatory pore; paired copulatory ducts chitinized, each running anteriorly to connect with seminal receptacle near genital operculum; seminal receptacle located lateromedially, half as long as double-somite, produced posteriorly with rounded posterior tip, tapering anteriorly; receptacle duct beneath copulatory duct, opening near inner corner of genital operculum.

Antennule symmetrical, 20-segmented; seventh (X) to ninth (XII) segments and 11th (XIV) and 12th (XV) segments only partly fused. Fusion pattern and armature ele-

ments as follows: I–IV–9 + 2 aesthetascs, V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2, IX–2 + (small) aesthetasc, X–2, XI–2 + aesthetasc; XII–2, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–XXVIII–12 + 2 aesthetascs (Fig. 13C). First (I–IV) to seventh segments fringed with long setules along posterior margin.

Antenna: first endopod segment without inner seta, second segment with 2 short inner setae of unequal lengths (Fig. 15D) and 5 terminal setae and reduced setule terminally; exopod indistinctly 7-segmented; setal formula 0,1,1,1,1,0,3. Mandibular palp (Fig. 13E,F): endopod absent; first exopod segment having relatively reduced seta, fifth segment carrying normal seta and vestigial element.

Maxillule: praecoxal arthrite (Fig. 13G) with 5 naked spines, 1 short process and row of long setules; coxal endite (Fig. 13G) carrying relatively long spinulose seta, fringed with numerous long setules along distal margin; basal seta lacking; endopod (Fig. 13G, indicated by arrowhead) rudimentary, almost fused with basis, unarmed. Maxilla: first praecoxal endite bearing thick naked seta and vestigial element, second praecoxal endite having 2 spinulose setae (Fig. 13H); basal spine (Fig. 13I) with 2 rows of minute spinules along ventral margin.

Maxilliped: sixth endopod segment (Fig. 15A,B) having elongate seta d with row of stout spinules whose base ornamented with lamellar projection (Fig. 15C), finely serrated, medial-length seta c and reduced setae a and b.

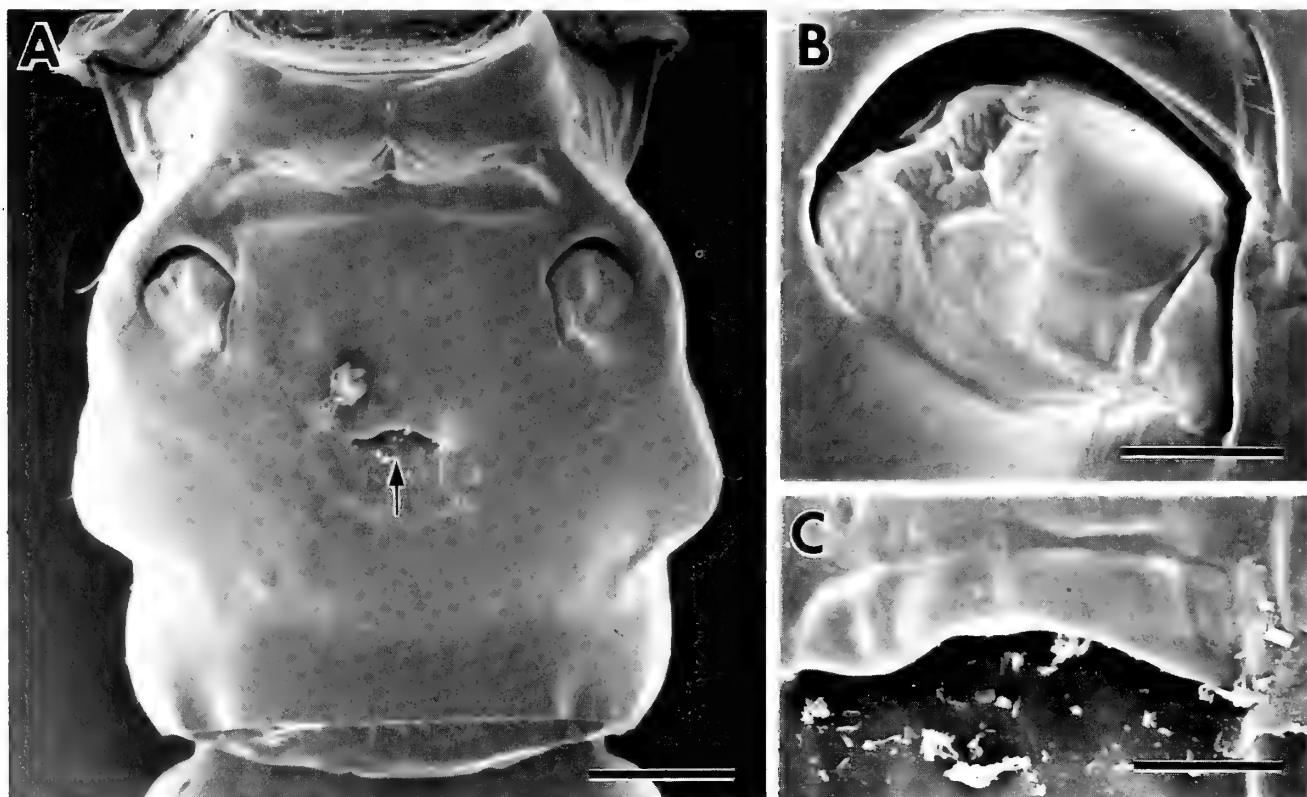


Fig. 14. *Arietellus plumifer*, female. SEM micrographs of genital double-somite of female. A, Genital double-somite, ventral view showing large copulatory pore (indicated by an arrow), scale bar = 100 μ m; B, Right gonopore, scale bar = 30 μ m; C, Copulatory pore, scale bar = 20 μ m.

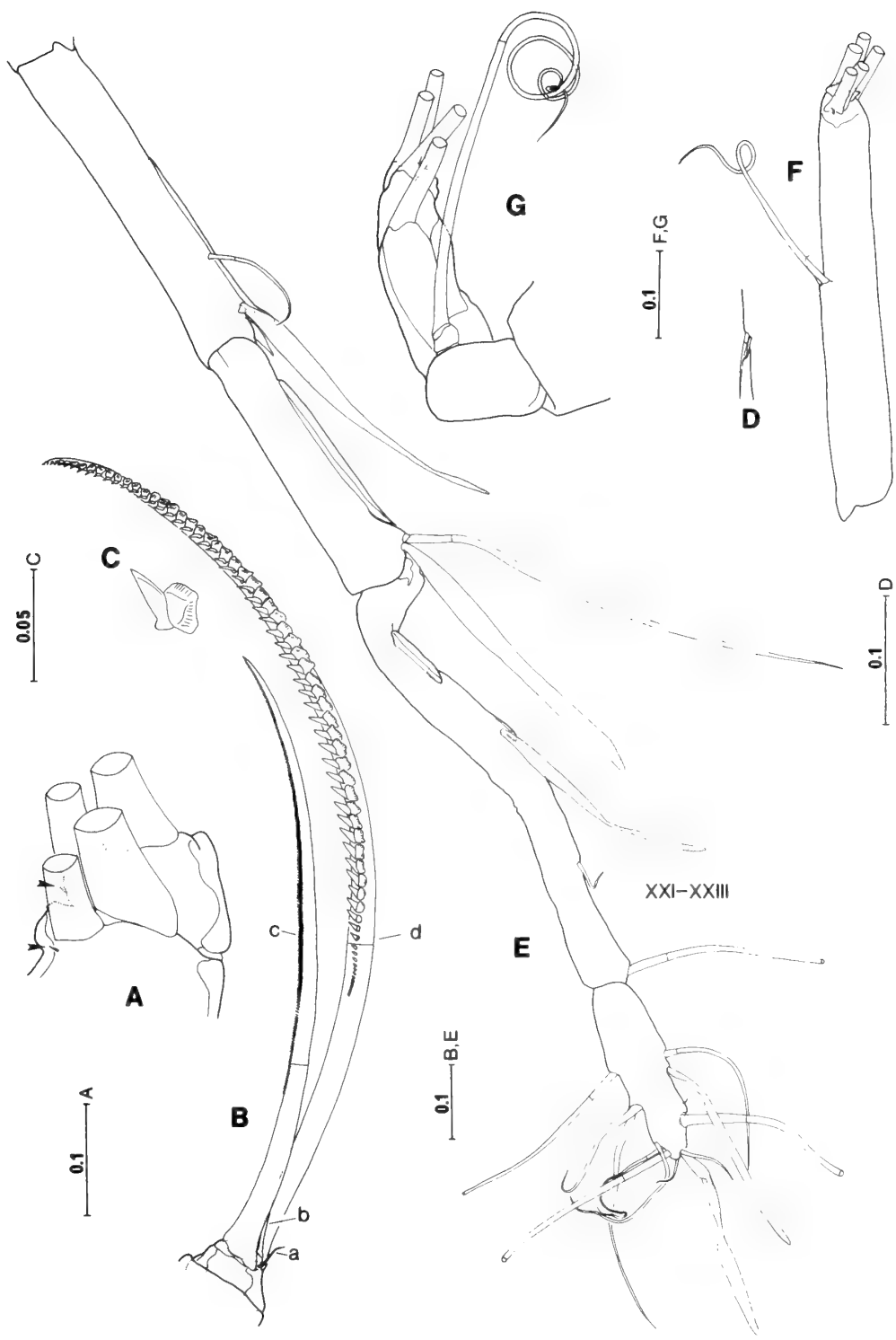


Fig. 15. *Arietellus plumifer*, female (A-D), male (E-G). A, Fourth and fifth endopod segments of maxilliped, innermost vestigial seta indicated by arrowhead; B, Sixth endopod segment of maxilliped; C, Spinule on seta d of sixth endopod segment of maxilliped; D, Mid-margin setae on second segment of antennary endopod; E, Left antennular segments XIX to XXVIII; F, Second endopod segment of antenna; G, Mandibular exopod. Scales in mm.

Leg 1: third exopod segment with 2 subterminal serrate spines.

Leg 5 (Fig. 17A): coxae incompletely fused with intercoxal sclerite; right basal seta extremely elongate; endopod represented by knob with 2 plumose setae; exopod incompletely fused with basis, 1-segmented, carrying 1 terminal spine.

Male. Left antennule (Fig. 15E) distinctly 19-segmented; 8th to 11th segments only partly fused near posterior margin; fusion pattern and armature elements as follows: I-IV-7 + 2 aesthetascs (I-3 + aesthetasc, II-1 + aesthetasc, III-1 + aesthetasc, IV-2 + aesthetasc), V-2 + aesthetasc, VI-2 + aesthetasc, VII-2 + aesthetasc, VIII-2 + aesthetasc, IX-2 + aesthetasc, X-1 + aesthetasc + process, XI-2 + aesthetasc, XII-1 + aesthetasc + process, XIII-1 + aesthetasc + process, XIV-1 + 2 aesthetascs + process, XV-1 + aesthetasc + process, XVI-2 + aesthetasc, XVII-2 + aesthetasc, XVIII-2 + aesthetasc, XIX-1 + aesthetasc + 2 processes, XX-1 + aesthetasc + process, XXI-XXIII-2 + aesthetasc + 2 processes (XXI-aesthetasc + 2 processes, XXII-1, XXIII-1), XXIV-XXVIII-11 + 2 aesthetascs (XXIV-1 + 1, XXV-1 + 1 + aesthetasc, XXVI-XXVIII-7 + aesthetasc); no suture visible between segments XXV and XXVI. First (I-IV) to sixth (IX) segments fringed with long setules along posterior margin.

Antenna: second endopod segment (Fig. 15F) with 1 short and 1 long seta medially and 5 setae and 1 vestigial setule terminally. Mandibular palp (Fig. 15G): first exopod segment with well-developed seta.

Leg 5 (Fig. 18L): both coxae fused to intercoxal sclerite to form common plate, right coxa almost fused with basis, left coxa completely separate from basis. Right leg: basal seta considerably elongate; endopod 1-segmented, spatulate; exopod indistinctly 3-segmented, first segment with 1 spine on outer corner, second incompletely fused with third, furnished with triangular process and 2 tufts of fine setules on inner corner and 1 spine on outer corner, third segment spatulate, with subterminal outer setule and terminal vestigial element. Left leg: endopod indistinctly 2-segmented, first and second segments unarmed; exopod indistinctly 3-segmented, first segment with 1 spine on outer corner, second segment incompletely fused with third, expanded inwards, bearing 1 subterminal outer spine, third segment small, having minute spinule and 2 spines almost fused basally with segment, terminal one bifid at tip.

Arietellus mohri (Björnberg, 1975), new combination (Figs 16A, 17C, 18A,B,F,H)

MATERIAL EXAMINED. ♀, U.S. National Museum, reference number USNM 150095.

BODY LENGTH. 6.40 mm (after Björnberg, 1975)

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Fig. 16A) as long as wide, with anterior pair of gonopores located ventrolaterally anterior to single ventromedial copulatory pore as in *A. plumifer*; copulatory ducts much more chitinized and wider than in *A. plumifer*, slightly asymmetrical, left duct divergent into blind tubule near left genital operculum; seminal receptacle the same shape as in *A. plumifer*.

Right antennule (left antennule missing distal segments) with fusion pattern and armature as *A. plumifer* except for missing elements. Antenna: first endopod segment unarmed, second segment with 2 inner setae of unequal length medially

and 5 setae and 1 vestigial setule terminally; exopod 7-segmented, setal formula: 0,1,1,1,0,3. Mandibular palp (Fig. 18A,B): endopod absent; exopod 5-segmented, first to fourth segments each with 1 seta, first segment with well-developed seta, fifth segment with 1 long seta and vestigial seta.

Maxillule: praecoxal arthrite with 5 naked spines and 1 bare process; coxal endite with 1 naked, thick seta terminally, fringed with long setules along ventral margin; coxal epipodite with 8 setae; endopod absent. Maxilla: first praecoxal endite with long, bare seta and 1 vestigial element; basal spine (Fig. 18F) with 2 rows of spinules along ventromedial margin. Maxilliped: fourth and fifth endopod segments each with only 2 well developed setae and lacking innermost seta, sixth segment (Fig. 18H) with vestigial seta a and short seta b.

Leg 1: basis with inner and, possibly, outer (scar present on outer margin) setae; third exopod segment with 2 lateral bipinnate spines. Leg 4, possibly, with 1 basal outer seta (scar present). Leg 5 (Fig. 17C): coxa and intercoxal sclerite almost fused, but suture line visible on left side; basis completely fused with coxa. Right leg: outer basal seta more elongate than left one; endopod represented by small knob with vestigial element at tip; exopod almost fused with basis, but suture visible only on anterior surface, unarmed, round. Left leg: basis with concavity on inner margin; outer basal seta thick, plumose; endopod reduced to low prominence with spinulose seta terminally; exopod almost completely fused with basis, unarmed, round.

REMARKS. Björnberg (1975) assigned one female of a new species collected from the southeastern Pacific (depths: 1932-3142 m) to the genus *Paraugaptilus*, probably because of the remarkably reduced fifth legs. The present re-examination revealed that it belongs to *Arietellus* not to *Paraugaptilus*, on the basis of the following characters: (1) the genital double-somite with single copulatory pore ventromedially; (2) the first, sixth and 10th antennular segments carrying 2, 1 and 1 aesthetascs, respectively; (3) the antennular segment XXVI-XXVIII with 7 setae and 1 aesthetasc; (4) the coxal endite of maxillule bearing 1 relatively well developed seta and fringed with long setules along ventral margin; (5) the second praecoxal endite of maxilla having 2 setae; (6) the endopodal setae of maxilla carrying sharp spinules with lamellar structure basally; (7) the fourth and fifth endopodal segments of maxilliped lacking innermost seta; (8) leg 4 without inner coxal seta; (9) leg 5 with distinct distal lobe derived from exopod; (10) the right basal seta of leg 5 considerably elongate.

Although Björnberg (1975) described the species in relatively great detail, the present re-examination of the holotype revealed that her description included several misinterpretations, particularly in the mouthparts and legs. These are amended in the present description.

Arietellus aculeatus (T. Scott, 1894) (Figs 16F,G,18D,E,O)

MATERIAL EXAMINED. ♀ and 2 ♂♂.

BODY LENGTH. ♀ 4.62 mm; ♂ 3.77, 3.79 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Left antennule similar to that of female *A. plumifer* except for following points: segments VIII and X each with minute aesthetasc; segment XIV carrying 2 setae

and 2 aesthetascs. Antenna: second endopod segment (Fig. 16G) with 2 short inner setae medially and 5 setae and 1 vestigial seta terminally. Mandibular palp (Fig. 18D): first exopod segment with reduced, short seta.

Male. Cephalosome separate from first pedigerous somite. Left antennule exhibiting same fusion pattern and armature elements as *A. plumifer* except for first segment: I-IV-7 + 7 aesthetascs (I-3 + aesthetasc, II-1 + 2 aesthetascs, III-1 + 2 aesthetascs, IV-2 + 2 aesthetascs). Antenna: second endopod segment (Fig. 16F) bearing 1 long and 1 short seta medially. Mandibular palp (Fig. 18E): first exopod segment with well-developed seta. Maxillule: endopod almost fused with basis, represented by small knob. Maxilliped: fourth and fifth endopod segments each having vestigial innermost seta, as in *A. plumifer*. Leg 5: left endopod (Fig. 18O) indistinctly 2-segmented, with suture visible on posterior surface; compound distal exopod segment of right leg with minute terminal element.

REMARKS. *A. aculeatus* exhibits sexual dimorphism in the antenna and mandibular palp, as does *A. plumifer*.

Arietellus setosus Giesbrecht, 1892 (Figs 16J,18I,M)

MATERIAL EXAMINED. ♂.

BODY LENGTH. 4.28 mm.

DESCRIPTION. Male. Cephalosome separate from first pedigerous somite. Left antennule with same fusion pattern and armature as *A. plumifer*. Antenna: exopod indistinctly 7-segmented; setal formula 0,1,1,1,1,0,3. Mandible: first exopod segment with normally developed seta. Maxillary endopod (Fig. 16J) represented by unarmed, small knob. Maxilla and maxilliped (Fig. 18I) as in *A. plumifer*. Leg 5: left endopod (Fig. 18M) indistinctly 2-segmented as in *A. plumifer*, first segment produced ventrally to rounded tip, second segment rising from inner side of first segment; terminal spine on third exopod segment of left leg almost completely fused to segment, subterminal spine incompletely coalesced with segment; distal compound exopod segment of right leg unarmed.

Arietellus pavoninus Sars, 1905 (Figs 16B,H,17B,18J)

MATERIAL EXAMINED. ♀.

BODY LENGTH. 5.00 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Fig. 16B) similar to that of *A. plumifer*, but readily distinguishable since seminal receptacle relatively much larger than in *A. plumifer*, over half length of genital double-somite.

Antennule with same fusion pattern and armature as *A. plumifer* except for absence of aesthetasc on segment IX (this aesthetasc may have been detached). Mouthparts similar to those of female *A. plumifer* except for maxillary endopod. Maxillule (Fig. 16H): endopod distinctly 1-segmented, bulbous with 1 bipinnate seta. Maxilliped (Fig. 18J): fourth and fifth endopod segments each with reduced innermost seta, sixth segment with reduced setae a and b. Leg 5 (Fig. 17B): coxae incompletely fused with intercoxal sclerite, in particular, more fused in right leg; endopod represented by 2 plumose setae not so produced as in *A. plumifer*; exopods

1-segmented, separate from basis, carrying 1 unipinnate spine terminally.

Arietellus simplex Sars, 1905 (Figs 16E,I,18N)

MATERIAL EXAMINED. ♂.

BODY LENGTH. 6.10 mm.

DESCRIPTION. Male. Cephalosome separate from first pedigerous somite. Left antennule with same fusion pattern and armature as *A. plumifer*.

Antenna: exopod (Fig. 16E) indistinctly 8-segmented; setal formula 0,1,1,1,1,0,0,3. Mandible: first exopod segment with normally developed seta. Maxillule: endopod represented by low knob, almost fused with basis (Fig. 16I). Maxilliped as in *A. plumifer*. Leg 5: left endopod (Fig. 18N) indistinctly 2-segmented, suture visible on both surfaces; terminal and subterminal spines on third exopod segment of left leg incompletely fused to segment, terminal spine with 4 minute spinules terminally; terminal spine of distal compound exopod segment of right leg unarmed.

Arietellus sp. (Figs 16C,D,17D,18C,G,K)

MATERIAL EXAMINED. ♀.

BODY LENGTH. 5.15 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Posterolateral angles of prosome asymmetrically produced into sharp lateral processes as in *A. giesbrechti* (see Sars, 1924, 1925), left process slightly longer and more produced than right. Genital double-somite (Fig. 16C) similar to that of *A. mohri* in having pair of laterally expanded copulatory ducts, but differing in presence of better developed muscles to genital operculum.

Left antennule with same segmentation and armature as *A. plumifer*. Antennary endopod: first segment unarmed, second (Fig. 16D) with 1 long and 1 short seta medially, and 5 setae and 1 vestigial element terminally. Mandibular palp (Fig. 18C) with relatively long seta on first exopod segment. Maxillary endopod completely fused with basis. Maxilla: basal spine (Fig. 18G) with 2 rows of spinules along ventral margin. Maxilliped (Fig. 18K): fourth and fifth endopod segments lacking innermost seta; sixth endopod segments with setae a and b reduced.

Leg 5 (Fig. 17D) similar to that of *A. mohri* with intercoxal sclerite, coxa, basis and both rami almost completely fused, but distinguishable by: seta on both endopods represented by low knob much better developed than in *A. mohri*; unarmed, lobate exopods more developed than in *A. mohri*; left basal seta longer than in *A. mohri*.

REMARKS. *Arietellus* sp., an as yet undescribed species, is most closely related to *A. mohri* in having synapomorphic characters such as no innermost seta on the fourth and fifth endopodal segments of maxilliped and the reduced leg 5.

Genus Rhipidophorus Edwards, 1891

TYPE SPECIES. *Rhipidophorus wilsoni* Edwards, 1891 (monotypic).

REMARKS. Fosshagen (1968) first pointed out the affinity of this genus with *Paramisophria*. Campaner (1977) later assigned the genus to the family Arietellidae. The genus,

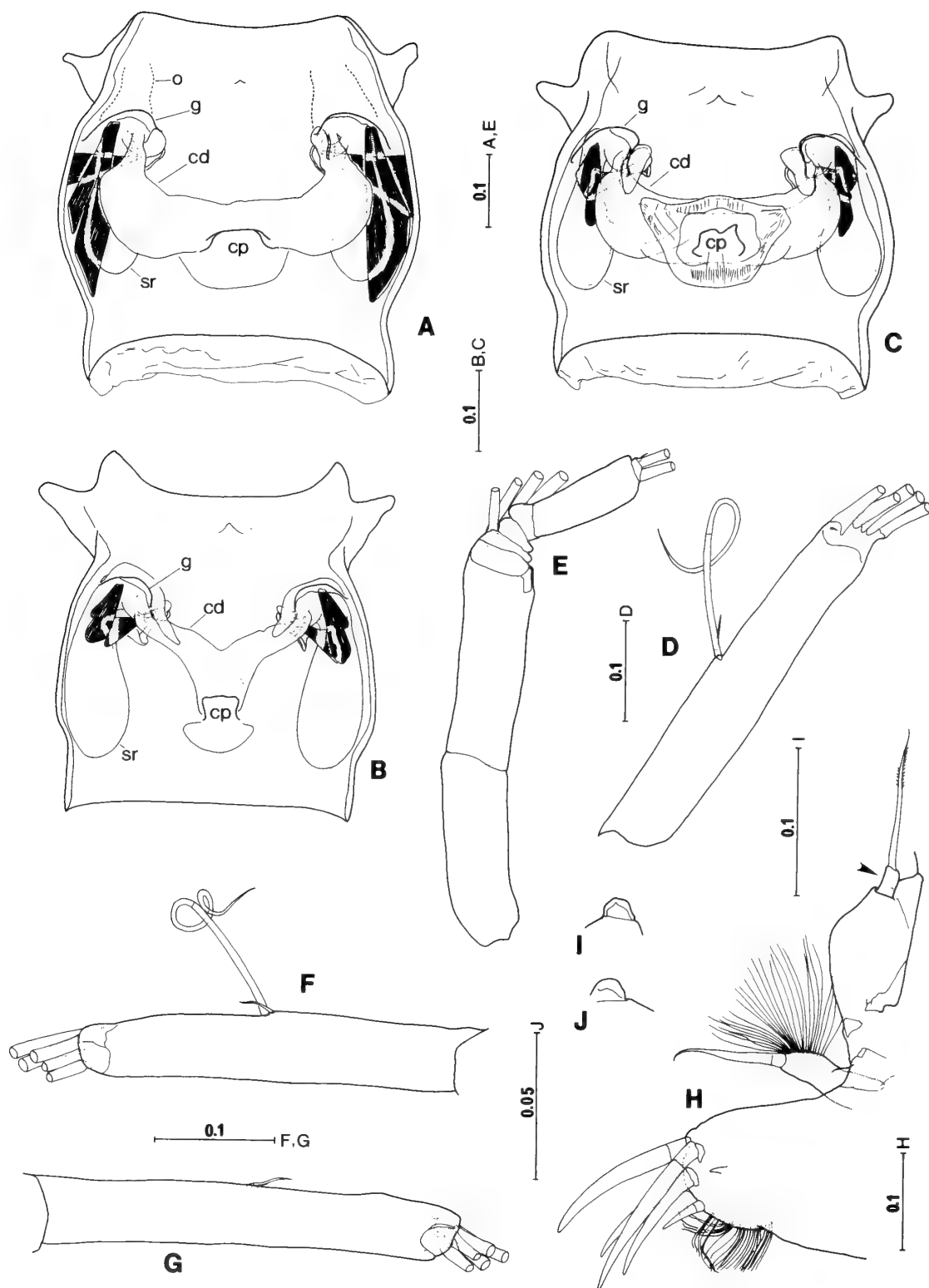


Fig. 16. *Arietellus mohri*, female (A); *A. pavoninus*, female (B,H); *A. sp.*, female (C,D); *A. simplex*, male (E,I); *A. aculeatus*, female (G), male (F); *A. setosus*, male (J). A-C, Genital double-somite, ventral view; D,F,G, Second endopod segment of antenna; E, Antennary exopod; H, Praecoxal arthrite, coxal endite and endopod of maxillule, endopod indicated by arrowhead; I,J, Maxillulary endopod. Scales in mm.

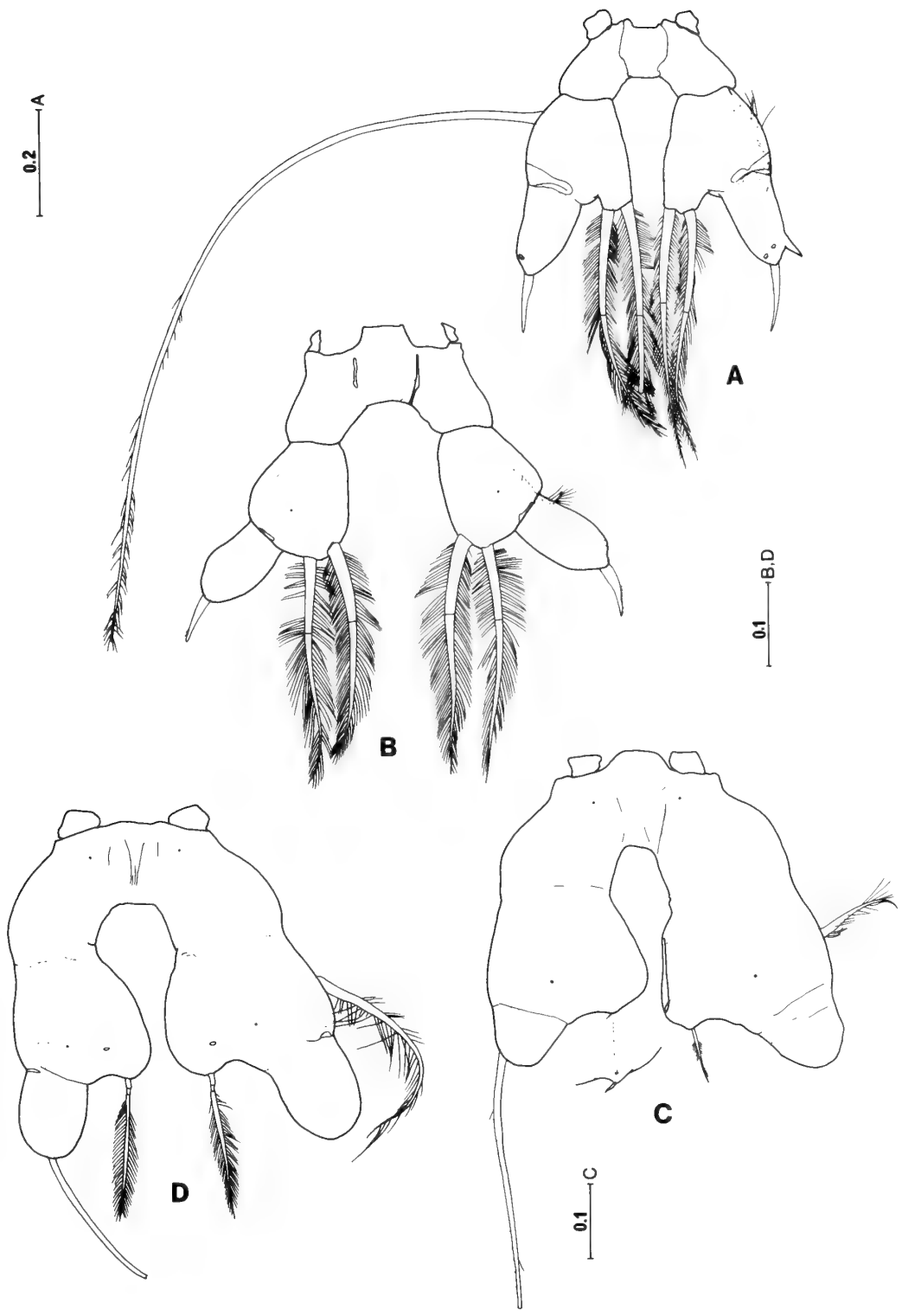


Fig. 17. Fifth legs of females of *Arietellus*. A, *A. plumifer*; B, *A. pavoninus*; C, *A. mohri*, vestigial element on right endopod represented by low knob incorporated in C; D, *A. sp.* Scales in mm.

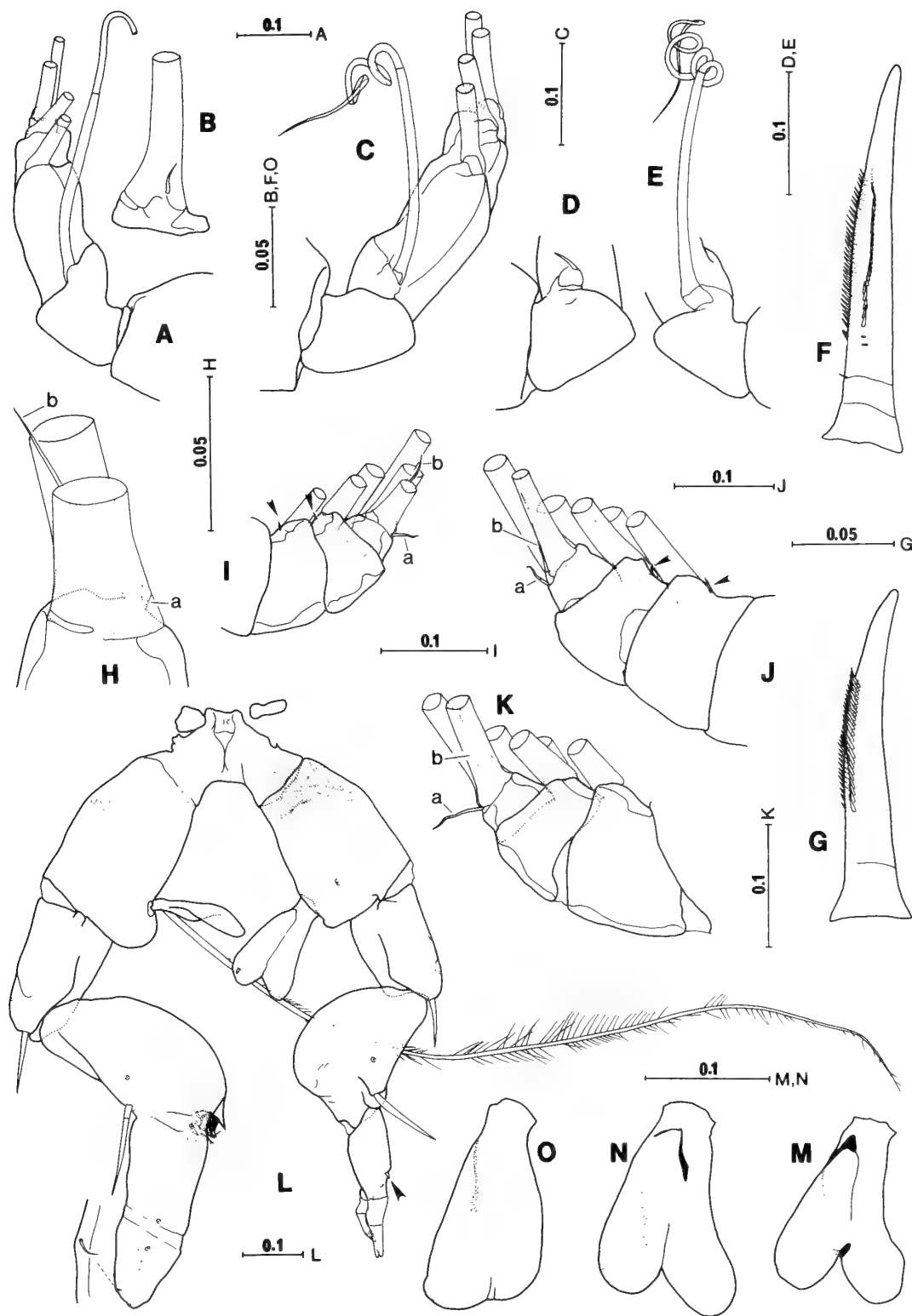


Fig. 18. *Arietellus mohri*, female (A,B,F,H); *A. sp.*, female (C,G,K); *A. aculeatus*, female (D), male (E,O); *A. setosus*, male (I); *A. pavoninus*, female (J); *A. plumifer*, male (L); *A. simplex*, male (N). A,C, Mandibular exopod; B, Fifth exopod segment of mandible; D,E, First exopod segment of mandible; F,G, Maxillary basal spine; H, Sixth endopod segment of maxilliped; I-K, Fourth to sixth endopod segments of maxilliped; L, Leg 5, anterior surface; M-O, Left endopod of leg 5. Scales in mm.

however, has peculiar characters in the mandibular palp, maxillule, maxilliped and leg 1 as indicated by Fosshagen (1968). We were unable to re-examine the male type specimen; it is deposited neither in the Berlin Zoological Museum (Dr. H.-E. Gruner, personal communication) nor at the University of Leipzig (Prof. K. Drössler, personal communication), and may no longer be extant. Since Edwards' (1891) description is not accurate enough to compare *Rhapidophorus* with the other genera, the present study does not include the genus in the cladistic analysis.

ECOLOGICAL NOTE. *Rhapidophorus* was found in the water-lung of a holothurian collected from the Bahamas, but was stated to be free-living (Edwards, 1891). The compact body, short antennule and stout legs suggest that it may originally have been hyperbenthic.

Genus *Paramisophria* T. Scott, 1897

DIAGNOSIS. The diagnostic characters of the genus have already been given in detail by Ohtsuka et al. (1993a). Supplemental diagnostic characters are given briefly here.

Body lengths of female and male approximately 0.6 to 3 mm and 0.6 to 2 mm, respectively. Female antennules: segments I–III fused; segments III and IV separate; segment IV without aesthetasc; segments XXIII and XXIV separate; posterior margin fringed with long setules from I to X. Male left antennule: segments II and III with 1 seta; segment XIII with 1 seta; segments XXI and XXII fused. Antenna: first endopod with inner medial seta, second segment with 3 inner setae at midlength, and 5 setae and 1 minute seta terminally; exopod indistinctly 8- or 9-segmented, segment VIII with seta. Mandibular gnathobase lacking or having a small tuft of setules medially, with 3 teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillary coxal epipodite with 8 setae. Maxilla: first praecoxal endite with 1–2 setae and vestigial element, second endite with 2 setae. Maxilliped: setal formula of endopod 1,4,4,3,3,4; innermost seta on fourth and fifth endopod segments not rudimentary, setae a and b on sixth segment not reduced.

TYPE SPECIES. *Paramisophria cluthae* T. Scott, 1897 (monotypic).

OTHER SPECIES. *P. spooneri* Krishnaswamy, 1959; *P. amphiola* Fosshagen, 1968; *P. giselae* (Campaner, 1977); *P. itoi* Ohtsuka, 1985; *P. variabilis* McKinnon and Kimmerer, 1985; *P. platysoma* Ohtsuka and Mitsuzumi, 1990; *P. japonica* Ohtsuka, Fosshagen and Go, 1991; *P. fosshageni* Othman and Greenwood, 1992; *P. reducta* Ohtsuka, Fosshagen and Iliffe, 1993; *P. galapagensis* Ohtsuka, Fosshagen and Iliffe, 1993; *P. cluthae* sensu Tanaka (1966).

REMARKS. *Parapseudocyclops* Campaner, 1977 was synonymized with the genus *Paramisophria* (Ohtsuka et al., 1991).

ECOLOGICAL NOTE. *Paramisophria* is mainly distributed in the near-bottom communities on the continental shelf (Ohtsuka et al., 1991), but also colonizes marine caves (Ohtsuka et al., 1993a).

Paramisophria japonica Ohtsuka, Fosshagen and Go, 1991 (Figs 19,20F)

MATERIAL EXAMINED. ♀.

BODY LENGTH. 1.85–2.08 mm (after Ohtsuka et al., 1991).

DESCRIPTION. Female. Genital double-somite (Fig. 19A) wider than long, with pair of gonopores anteroventrally and single copulatory pore ventromedially; seminal receptacle located lateromedially; copulatory duct thin.

Antennule: segments X to XII, and XIV and XV only partly fused near posterior margin; segments XXV and XXVI incompletely fused; segments I to X fringed by long setules along posterior margin; fusion pattern and armature as follows: I–III–7 + 2 aesthetascs (I–3 + aesthetasc, II–2, III–2 + aesthetasc), IV–2, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc).

Maxilla: first praecoxal endite with 1 seta and vestigial element, second with 2 finely spinulose setae (Fig. 19C); basal spine naked. Maxilliped: fourth and fifth segments (Fig. 19D) with relatively long innermost seta; sixth segment (Fig. 19E) with setae a and b not reduced.

Leg 5 (Fig. 20F): coxae and intercoxal sclerite almost completely fused to form common base; endopod almost completely fused to basis with fine suture visible on posterior surface; first exopod segment clearly separate from second; second and third exopod segments completely fused.

Paramisophria giselae (Campaner, 1977) (Fig. 20A–E)

MATERIAL EXAMINED. ♀, holotype, Museu de Zoologia, University of Sao Paulo, reference number 4004. ♀, paratype, Zoology Department, Instituto de Biociências, University of Sao Paulo, number 173.

BODY LENGTH. 2.55, 2.60 mm (after Campaner, 1977).

DESCRIPTION. Posterior lateral corners of second and third pedigerous somites asymmetrically produced: corners more sharply pointed on right side than on left. Genital double-somite (Fig. 20A) longer than wide; genital system similar to that of *P. japonica*, but differing in: copulatory pore located on right side; seminal receptacle located near gonopore; copulatory pore relatively thick.

Antennary exopod (Fig. 20B) indistinctly 9-segmented; terminal segment with 2 long plumose setae and vestigial seta. Mandibular gnathobase with small tuft of setules medially; 3 teeth on cutting edge, dorsalmost of which bifurcate at tip. Mandibular palp similar to that of *P. japonica*: endopod rudimentary, 1-segmented, with 2 setae of unequal lengths; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillule similar to that of *P. japonica* except for relatively long seta on coxal endite: praecoxal arthrite with 5 naked spines and 1 process; coxal epipodite with 8 setae; small basal seta present; endopod bulbous, 1-segmented with 3 setae of unequal lengths. Maxilla: first praecoxal endite (Fig. 20C) with 2 spinulose setae and rudimentary element, second (Fig. 20C) bearing 2 spinu-

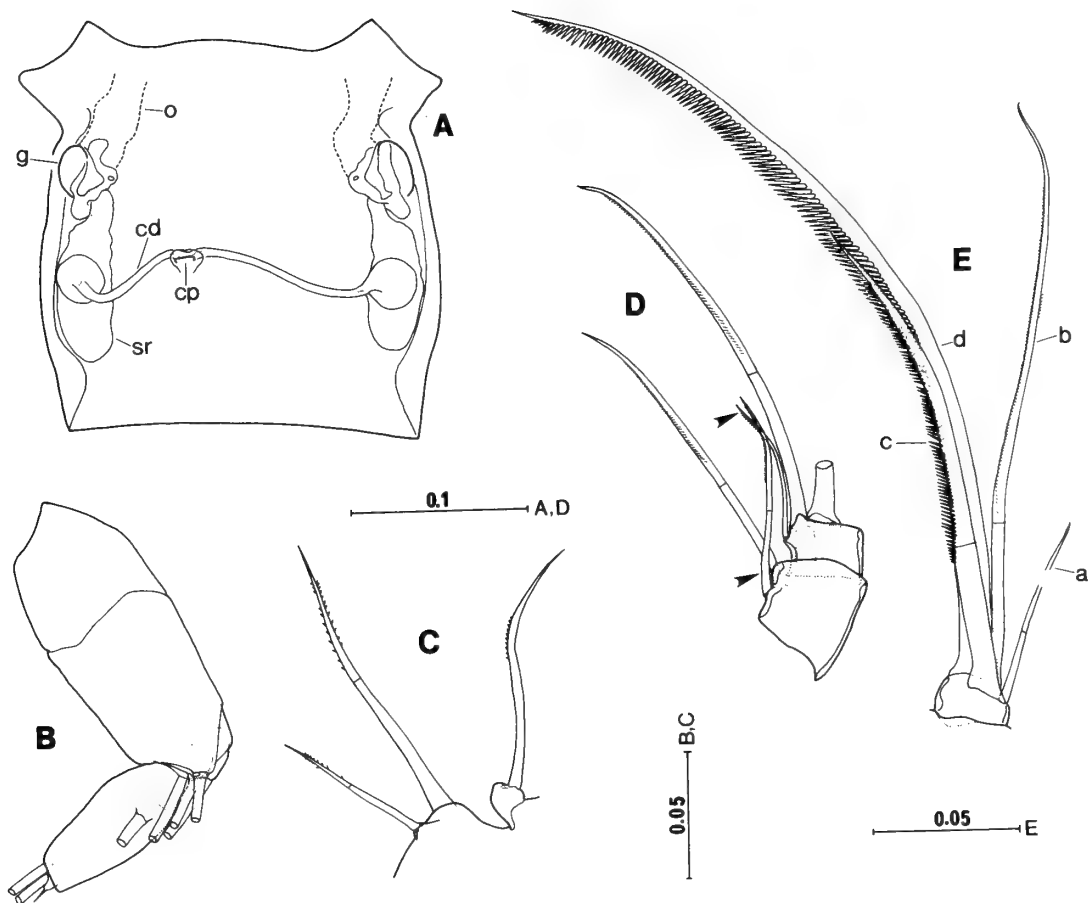


Fig. 19. *Paramisophria japonica*, female. A, Genital double-somite, ventral view; B, Antennary exopod; C, First and second praecoxal endites of maxilla; D, Fourth and fifth endopod segments of maxilliped; E, Sixth endopod segment of maxilliped. Scales in mm.

lose setae; basal spine (Fig. 20D) naked. Maxilliped with same setal formula as *P. japonica*.

Leg 5 (Fig. 20E): coxae and intercoxal sclerite clearly separate; setation and spinulation as in *P. japonica*; endopod completely fused to basis; exopod almost completely fused to basis with fine suture visible; first and second exopod segments fused with suture clearly visible on posterior surface; second and third exopod segments completely fused.

REMARKS. Re-examination of the holotype and paratype revealed the following: (1) since the antennules of both types are missing (the proximal half remains on one side only), we were unable to check the fusion and armature patterns; (2) the terminal segment of the antennary exopod has only 2 developed setae plus 1 minute seta although 3 developed setae were shown in the original description (Campaner, 1977); (3) the dorsalmost tooth on the mandibular gnathobase is bicuspid although it was originally drawn as monocuspid (Campaner, 1977); (4) the terminal segment of the mandibular exopod has 2 relatively well developed setae (one about 25% shorter than the other); (5) the setae on the mandibular endopod are missing but there are 2 scars visible, of different sizes, which suggests 2 unequal setae; (6) the coxal epipodite of the maxillule of the holotype is damaged: 5 long setae are present, then a gap due to damage, then a short seta; although the gap does not show clean scars where setae were broken off, the gap is only big enough for 2 setae – giving a total of 8 setae as in the paratype; (7) the first to sixth

endopodal segments of the maxilliped bearing 1, 4, 4, 3, 3 and 4 setae, respectively; (8) no seta originating from the posterior surface of the first exopodal segment of leg 4.

Paramisophria reducta Ohtsuka, Fosshagen and Iliffe, 1993

MATERIAL EXAMINED. ♂, allotype, The Natural History Museum, BM (NH) Reg. No 1992. 1093.

BODY LENGTH. 1.60 mm (after Ohtsuka et al., 1993a).

DESCRIPTION. Male. Left antennule: segments XXI to XXIII, XXIV and XXV, and XXVI to XXVIII completely fused; segments XXIII and XXIV, and XXV and XXVI incompletely fused; fusion pattern and armature elements as follows: I–IV–7 + 4 aesthetascs (I–3 + aesthetasc, II–1 + aesthetasc, III–1 + aesthetasc, IV–2 + aesthetasc), V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–1 + aesthetasc + process, XI–2 + aesthetasc, XII–1 + aesthetasc + process, XIII–1 + aesthetasc + process, XIV–1 + aesthetasc + process, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–1 + aesthetasc + 2 processes, XX–1 + aesthetasc + process, XXI–XXIII–2 + aesthetasc + 2 processes (XXI–aesthetasc + 2 processes, XXII–1, XXIII–1), XXIV–XXV–4 + aesthetasc (XXIV–1 + 1, XXV–1 + 1 + aesthetasc), XXVI–XXVIII–8 + 2 aesthetascs.

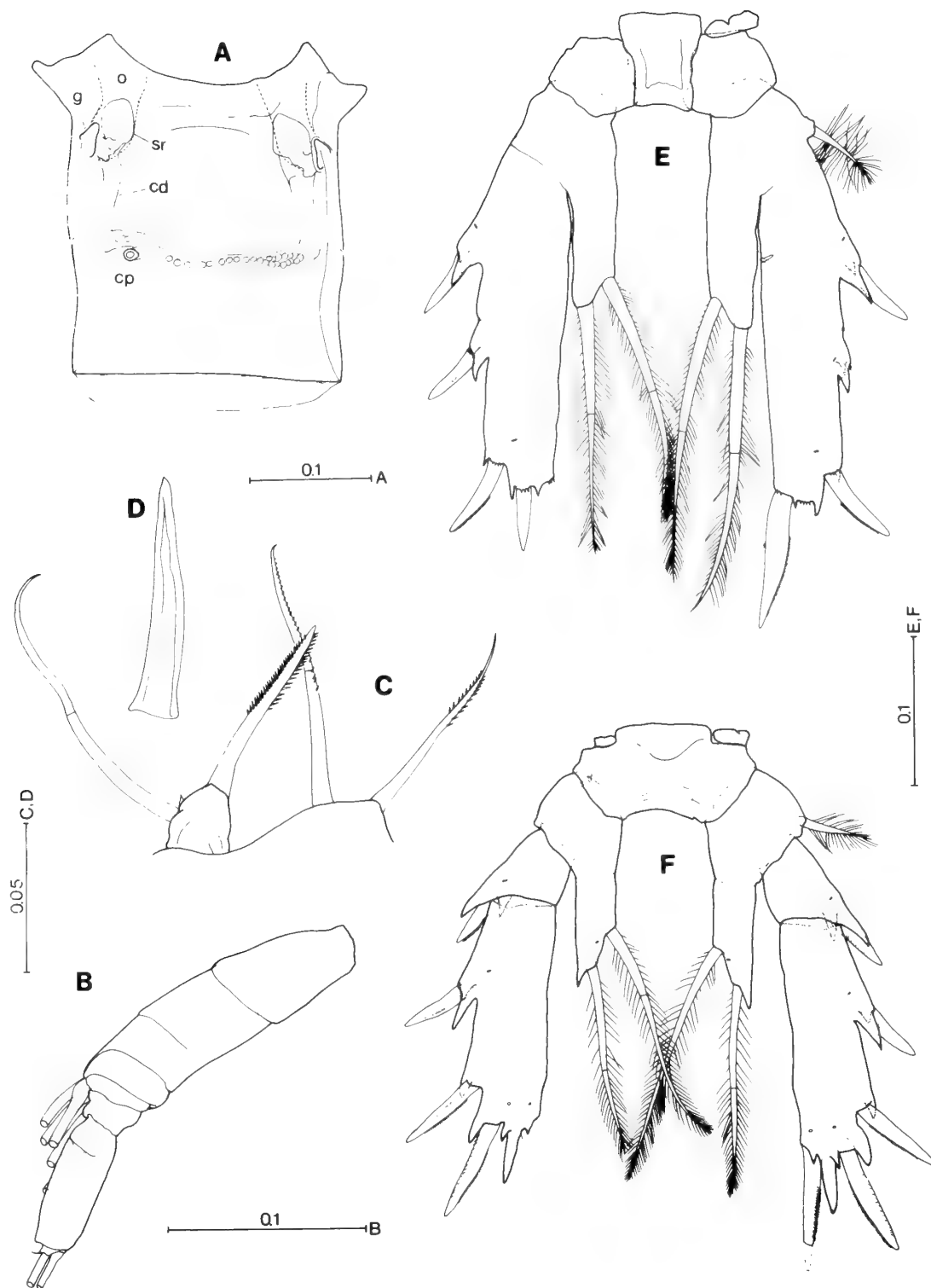


Fig. 20. *Paramisophria giselae*, female (A-E); *P. japonica*, female (F). A, Genital double-somite, ventral view; B, Antennary exopod; C, First and second praecoxal endites of maxilla; D, Basal spine of maxilla; E, F, Leg 5, anterior surface. Scales in mm.

REMARKS. The fusion pattern of the antennular segments is slightly different from the male of *P. japonica* in which segments XXI and XXII are incompletely fused whereas segments XXIII and XXIV are separate.

Genus *Metacalanus* Cleve, 1901

DIAGNOSIS (emended). Female. Body compact, small, measuring approximately 1 mm in body length. Prosome oval in dorsal view, not produced frontally; cephalosome and first pedigerous somite separate or weakly fused; posterior corners of last prosomal somite produced to form ventrolateral lobe, without dorsolateral processes; urosome short, less than one-third length of prosome. Genital double-somite wider than long, with ventrolateral pair of gonopores or only right gonopore (left reduced) located posteriorly; paired copulatory pores small, located near inner corner of genital aperture (in the case of reduction of left gonopore, only right copulatory pore present); anal operculum either developed, triangular or not. Caudal rami symmetrical, longer than wide, with seta II reduced or completely lacking; seta III relatively small.

Antennules asymmetrical, left longer than right and reaching to end of prosome, different in fusion pattern and armature; indistinctly 18- or 20-segmented in right antennule, 16- or 18-segmented in left; posterior proximal margin lacking long setules; segments I–IV up to VI; segments IX and X fused; segments XII to XIV fused in left; segments II, VII and IX with 1 or 2 setae; segment XIII with 1 seta; segments II, IV, VI, VIII and X lacking aesthetasc; segments V, XII and XIII with or without aesthetasc; compound segment XXVI–XXVIII with 8 setae and aesthetasc. Antenna: first endopod segment with 1 inner seta, second with 2 setae medially and 5 setae terminally; exopod indistinctly 7-segmented. Mandibular gnathobase lacking tuft of setules; 4 teeth on cutting edge, dorsalmost of which trifold at tip. Mandibular palp: endopod almost fused to basis, represented by small knob with 1 or 2 setae terminally; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillule: praecoxal arthrite with 0–2 spines; coxal endite with or without 1 short seta; coxal epipodite with 5 setae; endopod absent or 1-segmented, bulbous with 1 seta. Maxilla: first praecoxal endite with 1 seta and 1 rudimentary element; basal spine with 2 rows of minute spinules proximally; endopodal setae with row of spinules along inner margin. Maxilliped: setal formula on first to sixth endopod segments 1,4,4,3,3,4; innermost seta on fourth and fifth endopod segments not reduced; only distalmost seta on these segments well-chitinized and long; setae a and b on sixth endopod segment not reduced.

Third exopod segment of leg 1 with single outer spine. Leg 5: coxae separate from intercoxal sclerite; endopod represented by 1 seta or completely absent; exopod and basis fused or separate; exopod either 1-segmented, with 1–3 spines or represented by small knob bearing 1 seta.

Male. Body as in female, measuring less than 1 mm in body length. Left antennule 16-segmented; segments I–IV, IX–X and XII–XIV fused; segment XIII without seta; segment XXI separate from XXII. Leg 5: coxae and intercoxal sclerite fused; basis separate from coxa; endopod absent; exopod 3-segmented, third segment with large seta almost fused with segment.

TYPE SPECIES. *Metacalanus aurivilli* Cleve, 1901 (= *Scottula*

ambariae Binet and Dessier, 1968) (monotypic).

OTHER SPECIES. *M. inaequicornis* (Sars, 1902); *M. acutioperculum* Ohtsuka, 1984; *M. curvirostris* Ohtsuka, 1985; *M. species 1* and *2* from Okinawa.

REMARKS. *Metacalanus* was recognized as a senior synonym of *Scottula* Sars, 1902 by Campaner (1984).

ECOLOGICAL NOTE. *M. aurivilli* seems to be epipelagic in subtropical waters in the Indo-West Pacific (cf. Greenwood, 1978). Other species are hyperbenthic in shallow waters in temperate and subtropical regions (cf. Sars, 1903; Ohtsuka, 1984, 1985), or are marine cave-dwellers (Ohtsuka et al., 1993a).

Metacalanus species 1 (Figs 21B–I, 23, 25A, 26A–G)

MATERIAL EXAMINED. 4 ♀♀ and ♂.

BODY LENGTH. ♀ 0.81, 0.83, 0.83, 0.84 mm; ♂ 0.77 mm.

DESCRIPTION. Female. Cephalosome only partly fused with first pedigerous somite. Genital double-somite (Figs 21B, 23B) wider than long, asymmetrical, left gonopore and copulatory pore completely absent; right gonopore located near posteroventral margin of double somite, anterior half opening, covered by oval flap, possibly derived from leg 6; outer half gonopore frilled with cuticular flap (Fig. 23A); copulatory pore (Fig. 23C) small, oval in shape, approximately 4.0 µm in long axis and 1.0 µm in short axis, near inner distal corner of gonopore (copulatory pore blocked by spermatophore remnant); single seminal receptacle large, about half width of somite, located ventromedially; copulatory duct short, curved. Anal operculum triangular as in *M. acutioperculum*.

Antennules asymmetrical, left longer than right, different in fusion pattern and armature (see Fig. 22). Right antennule: segments X to XII and XIV and XV fused only partly near posterior margin; fusion pattern and armature as follows: I–IV–9 + 2 aesthetascs (I–3 + aesthetasc, II–2, III–2 + aesthetasc, IV–2), V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2, IX–X–4 + aesthetasc (IX–2 + aesthetasc, X–2), XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–1 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–1 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc). Left antennule different from right one in following: segments XII to XIV fused, with 5 setae and 2 aesthetascs (XII–2, XIII–1 + aesthetasc, XIV–2 + aesthetasc); segment XX with 2 setae and aesthetasc.

Antenna: exopod (Figs 21E, 25A) indistinctly 7-segmented; setal formula 0,1,1,1,1,1,3 (2 setae and vestigial element). Mandibular palp (Fig. 21F): endopod 1-segmented, almost fused with basis, with 2 setae of unequal lengths; first exopod segment carrying long seta, fifth segment bearing 2 normal setae of unequal lengths. Maxillule (Fig. 21G): praecoxal arthrite with 2 slender setae; coxal endite having 1 short seta; coxal epipodite having 5 setae; basal seta absent; endopod (indicated by arrowhead) 1-segmented, bulbous, with short seta terminally. Maxilla: first and second praecoxal endites with 1 seta plus 1 vestigial element and 2 setae respectively (Fig. 21H); basal spine (Fig. 21I) with 2 rows of short spinules proximally. Maxilliped: fourth and fifth endopod, segments

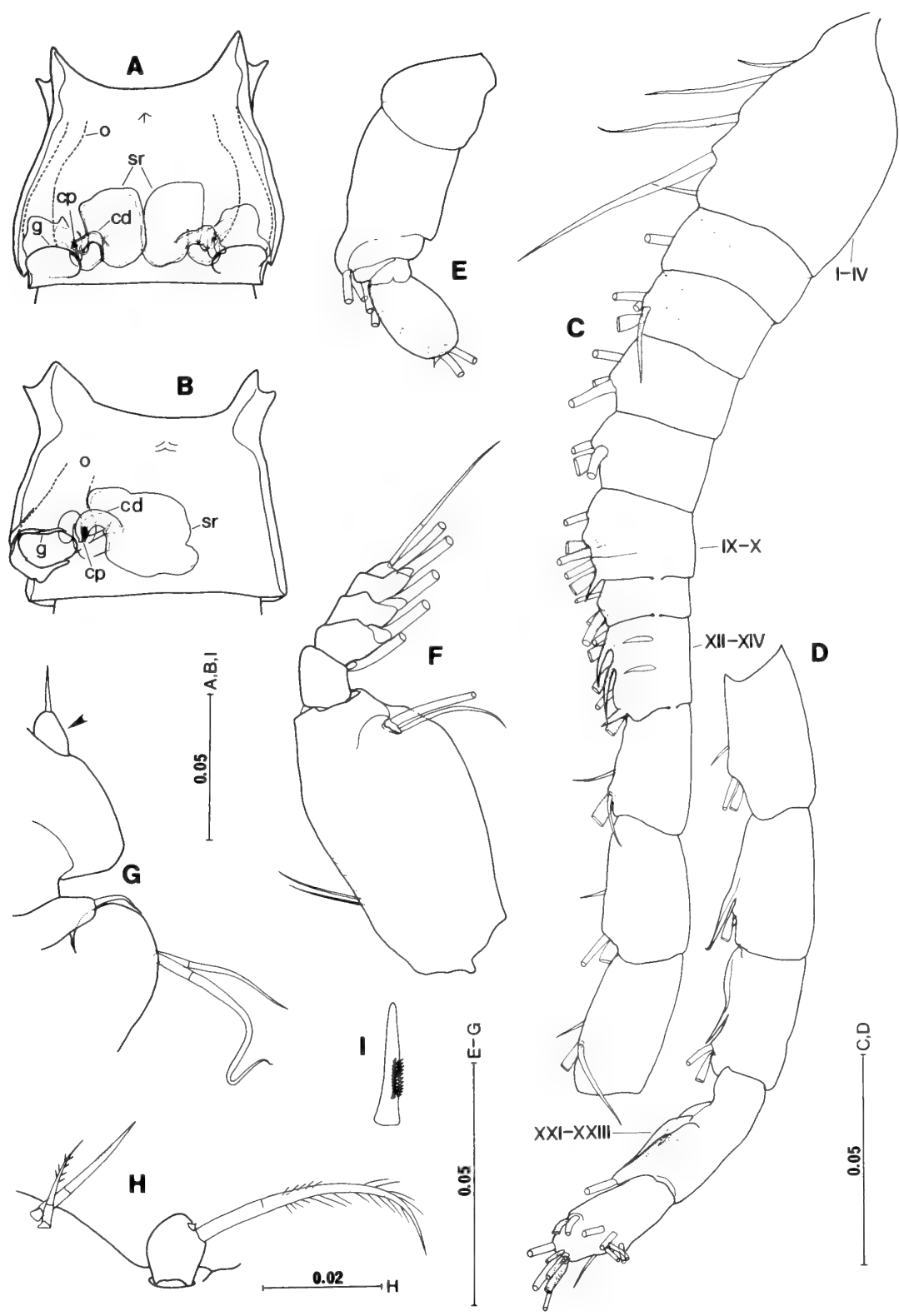


Fig. 21. *Metacalanus* sp. 1, female (B,E-I), male (C,D); *Metacalanus* sp. 2, female (A). A,B, Genital double-somite, ventral view; C, Left antennular segments I to XVII; D, Left antennular segments XVIII to XXVIII; E, Antennary exopod; F, Mandibular palp; G, Prae-coxal arthrite, coxal endite and endopod of maxillule, endopod indicated by arrowhead; H, First and second praecoaxal endites of maxilla; I, Basal spine of maxilla. Scales in mm.

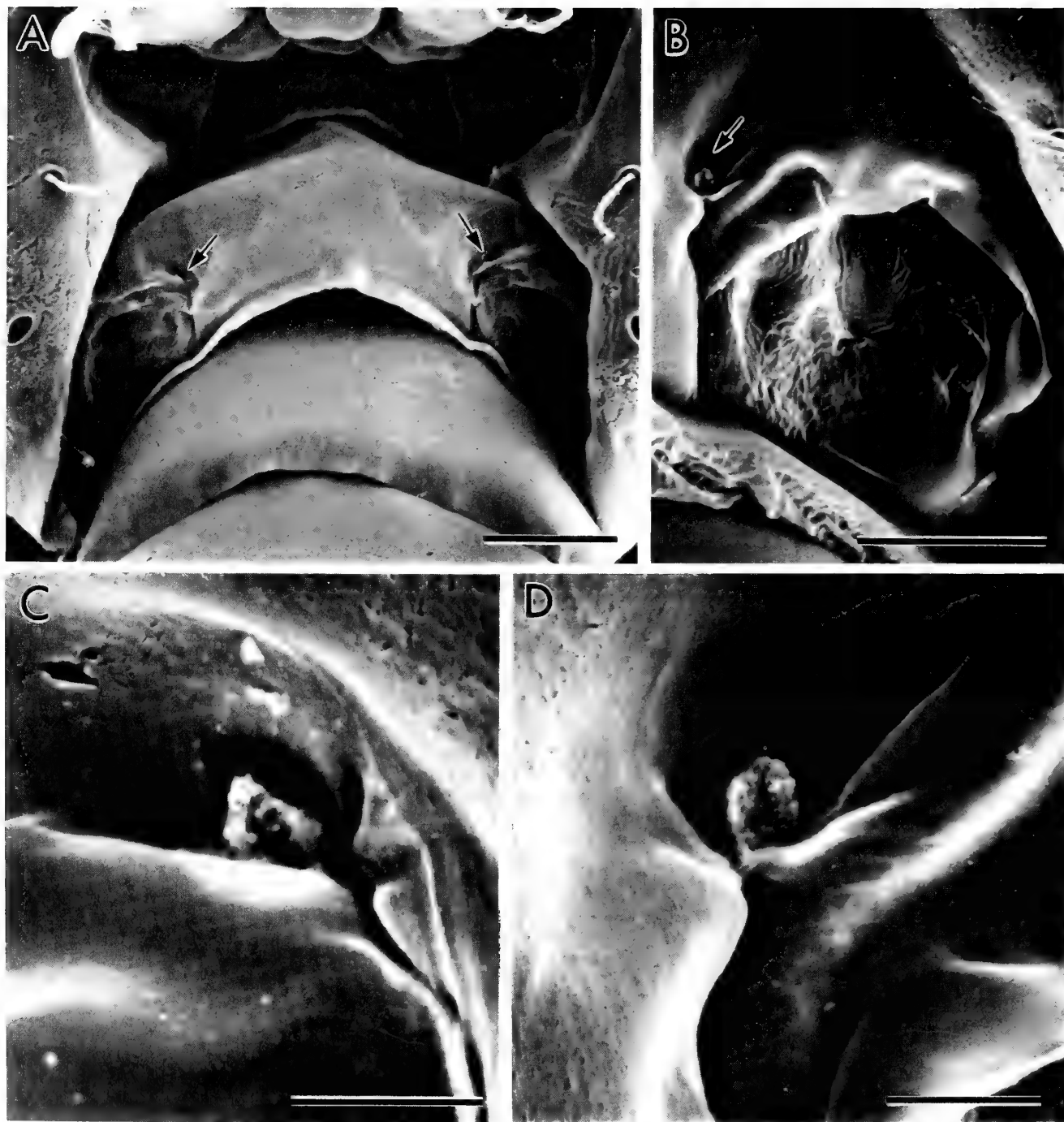


Fig. 24. *Metacalanus* sp. 2, female. SEM micrographs of genital double-somite. A, Genital somite, copulatory pores indicated by arrows, scale bar = 20 μm ; B, Left gonopore and copulatory pore (indicated by an arrow), scale bar = 10 μm ; C, Right copulatory pore, scale bar = 2 μm ; D, Left copulatory pore, scale bar = 2 μm .

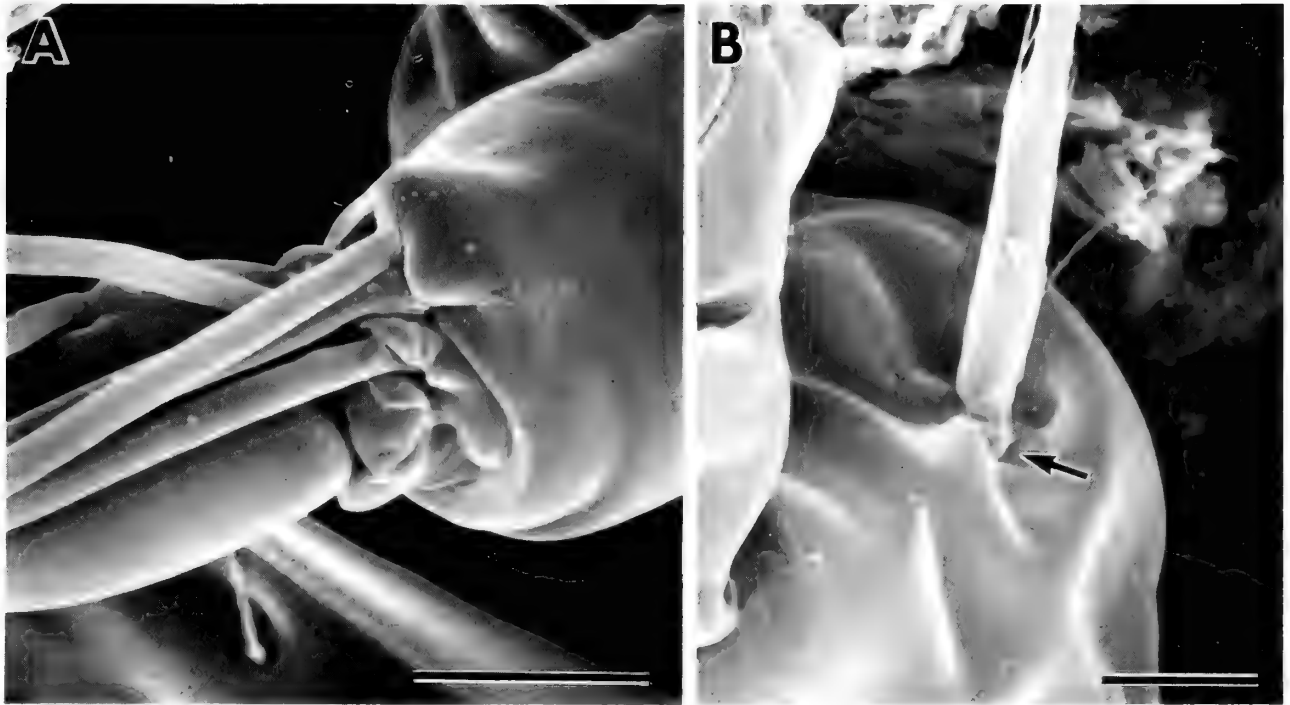


Fig. 25. *Metacalanus* sp. 1, female (A); *Metacalanus* sp. 2, female (B). SEM micrographs of mouthparts. A. Detail of segments IV to VIII of antennary exopod, scale bar = 10 μ m; B. Mandibular endopod, indicated by arrow, scale bar = 5 μ m.

Metacalanus species 2 (Figs 21A, 24, 25B, 26H)

MATERIAL EXAMINED. 4 ♀♀.

BODY LENGTH. 0.84, 0.84, 0.86, 0.88 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Lateral lobe of last prosomal somite produced backwards reaching halfway along second urosomal somite (Fig. 24A). Genital double-somite (Figs 21A, 24A) wider than long, symmetrical, with paired gonopores and copulatory pores located ventrolaterally near posterior end of somite; each gonopore lacking outer cuticular lateral flap found in *M. species* 1, anterior half opening, covered by oval flap; copulatory pore (Fig. 24C,D) small, round, ca. 1.4 μ m in diameter, located near anterior inner corner of gonopore (spermatophore remnant attached to opening). Internal genital system similar to that of *M. species* 1. Anal operculum triangular as in *M. species* 1.

Antennule asymmetrical, left longer than right, different in fusion pattern and armature (see Fig. 22). Right antennule: segments X to XI, and XIV and XV only partly fused near posterior margin; fusion pattern and armature as follows: I–VI–12 + 2 aesthetascs (I–3 + aesthetasc, II–1, III–2 + aesthetasc, IV–2, V–2, VI–2), VII–1 + aesthetasc, VIII–1, IX–X–3 + aesthetasc (IX–1 + aesthetasc, X–2), XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–1 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–1 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc). Left antennule: segments X and XI partly fused near posterior margin; suture between segments XI and XII visible on both surfaces, XII and XIII only on one surface,

XIII and XIV completely fused; fusion pattern and armature as follows: I–V–10 + 2 aesthetascs (I–3 + aesthetasc, II–1, III–2 + aesthetasc, IV–2, V–2), VI–2, VII–1 + aesthetasc, VIII–1, IX–X–3 + aesthetasc (IX–1 + aesthetasc, X–2), XI–XIV–7 + 2 aesthetascs (XI–2 + aesthetasc, XII–2, XIII–1, XIV–2 + aesthetasc), XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc).

Antenna with same segmentation and setation as *M. species* 1. Mandibular palp: endopod (Fig. 25B) rudimentary, 1-segmented, with 1 plumose seta; exopod with setation as in *M. species* 1. Maxillule: praecoxal arthrite without elements; coxal edite with short seta; coxal epipodite with 5 setae; no basal seta; endopod represented by small, unarmed knob. Maxilla and maxilliped as in *M. species* 1.

Legs 1 to 4 with same segmentation and setation as *M. sp.* 1. Leg 5 (Fig. 26H): coxae separate from intercoxal sclerite; right basal seta thicker than left; endopod absent; right and left exopods each 1-segmented, bulbous, with spiniform seta terminally.

REMARKS. The fifth leg of this as yet undescribed species resembles that of *M. curvirostris* but it can be distinguished from the latter by the smaller body, the longer antennules, and by differences in the mouthparts.

Genus Paraugaptilus Wolfenden, 1904

DIAGNOSIS (emended). Female. Body relatively large, measuring about 3 mm in total length. Prosome: cephalosome narrowed anteriorly, separate from or weakly fused with first

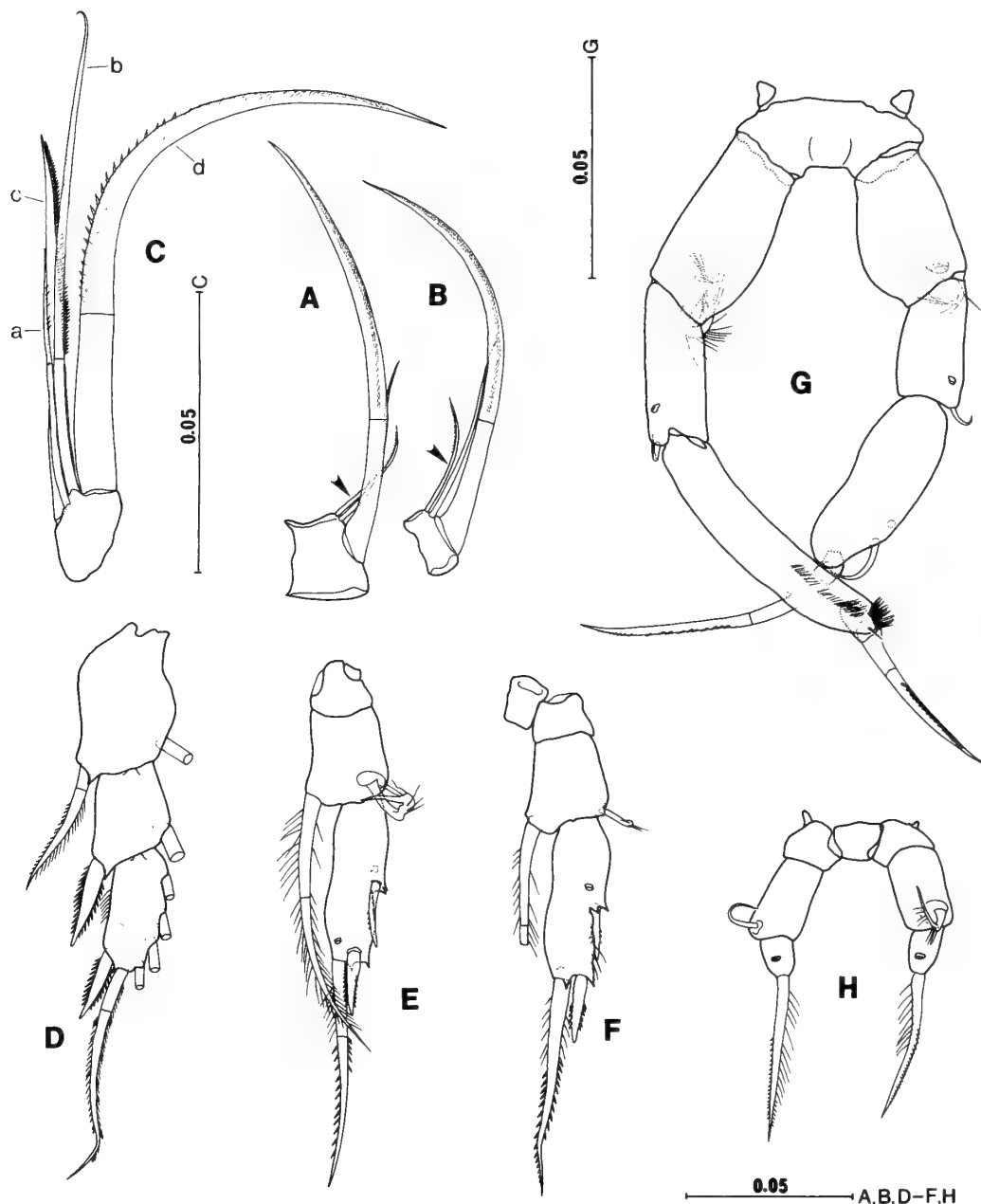


Fig. 26. *Metacalanus* sp. 1, female (A-F), male (G); *Metacalanus* sp. 2, female (H). A. Fourth endopod segment of maxilliped, innermost seta indicated by arrowhead; B. Fifth endopod segment of maxilliped, innermost seta indicated by arrowhead; C. Sixth endopod segment of maxilliped; D. Exopod of leg 1, anterior surface; E. Right leg 5, posterior surface; F. Left leg 5, anterior surface; G. Leg 5, anterior surface; H. Leg 5, posterior surface. Scales in mm.

pedigerous somite; last pedigerous somite with short prominence or curved process dorsally and weakly developed lobe laterally on each side. Genital double-somite with pair of gonopores located anteroventrally; copulatory pores asymmetrically distributed posteroventrally, each copulatory duct heavily chitinized; seminal receptacle relatively small. Caudal rami symmetrical, longer than wide, with setae II and III normally developed.

Antennule symmetrical or slightly asymmetrical in ornamentation of terminal segments (outer seta on segments XXV and XXVI with thicker setules in one antennule than in other) and in length, left slightly longer than right, 20-segmented; segments I to IV fused; segments XXIII–XXVIII fused; segments II, IV, VI, VIII–X, XII and XIII

lacking aesthetasc; segment XIII with 2 setae; compound segment XXVI–XXVIII with 7 setae and 1 or 2 aesthetascs. Antenna: first endopod segment without inner seta, second segment bearing 1 seta medially, and 5 setae and vestigial seta terminally; exopod indistinctly 6-segmented, sixth segment rudimentary, unarmed. Mandibular gnathobase with tuft of setules; 3 teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: endopod absent; first exopod segment bearing vestigial seta, outer seta on fifth segment vestigial. Maxillule: praecoxal arthrite with 5 spines; coxal endite bearing no seta; coxal epipodite with 8 setae; endopod absent. Maxilla: first and second praecoxal endite bearing 1 seta and 1 rudimentary element, and 1 seta, respectively; basal spine bipinnate; endopodal setae with triangular

spinules along inner margin. Maxilliped: setal formula of endopod 1,4,4,3,3,4; setae a and b on sixth endopod segment reduced; seta c heavily chitinized, terminal inner spinules fused to seta to form serrate margin.

Third exopod segment of leg 1 with 2 outer spines. Leg 4 with minute inner coxal seta, in addition to basal seta. Leg 5 rudimentary, represented by a plate with proximal (basal) seta and terminal or subterminal (endopod) seta.

Male. Body as in female, measuring around 3 mm in length. Left antennule 19-segmented; only first segment fringed with setules along posterior margin; segments II and III with seta; segment XIII with 2 setae; segment XXI and XXII fused; compound segment XXIV–XXV with large cuticular process; segment XXVI–XXVIII with 7 setae and aesthetasc.

Antenna: second endopod segment relatively shorter than in female, with 1–2 setae medially; exopod indistinctly 6- or 7-segmented, segment VIII with or without seta, terminal compound segment (IX–X) completely or incompletely fused with segment VIII, bulbous, unarmed. Mandibular palp: first exopod segment with well-developed seta.

Leg 5: coxae fused with intercoxal sclerite; basis and coxa separate in left leg and incompletely fused in right. Right leg: endopod 1-segmented, rudimentary, unarmed; second exopod segment expanded inwards, almost completely fused with third to form compound segment, tapering distally, carrying proximal seta and subterminal setule along outer margin. Left leg: endopod 1-segmented, unarmed; exopod 3-segmented, last 2 segments almost fused, second exopod segment swollen medially, third segment with 2 stout long, outwardly-directed process terminally.

TYPE SPECIES. *Paraugaptilus buchani* Wolfenden, 1904 (monotypic).

OTHER SPECIES. *P. similis* A. Scott, 1909; *P. meridionalis* Wolfenden, 1911; *P. mozambicus* Gaudy, 1965; *P. archimedi* Gaudy, 1973; *P. bermudensis* Deevey, 1973; *P. buchani* sensu Bradford, 1974.

REMARKS. In *P. bermudensis* sexual dimorphism is exhibited in the mouthparts and leg 1 (Deevey, 1973): second endopodal segment of antenna carrying 1 short seta in female and 1 long plus 1 short seta in male, at midlength of the segment; relative lengths of endopod and exopod of antenna; antennary exopodal segment VIII unarmed in female, but bearing long seta in male; first exopodal segment of mandible unarmed (vestigial seta overlooked by Deevey (1973)) in female but with well-developed seta in male; endopod of leg 1 indistinctly 3-segmented in female but distinctly in male. Except for leg 1 the sexual dimorphism in *P. bermudensis* is also found in *P. similis* (present study).

Since the superfamily Arietelloidea Sars, 1902 generally exhibits distinctly 3-segmented rami in legs 1–4 (Andronov, 1974; Park, 1986) and no other congeners show such fusion in endopod of leg 1, the incomplete fusion of the endopodal segments in the female seems to be autapomorphic in *P. bermudensis*. *P. buchani* exhibits sexual dimorphism only in the relative lengths of the antennary rami and in the setation of the mandibular palp (Deevey, 1973; present study).

Brodsky (1950) mentioned, in his definition of *Paraugaptilus*, that the left antennules of females are possibly longer than the right, but *P. similis* has antennules of nearly equal length (Scott, 1909; present study).

ECOLOGICAL NOTE. *Paraugaptilus* is mainly distributed within the upper 1000 m, in particular, between 500 and 1000 m depths (Deevey, 1973). The genus appears to be meso- and bathypelagic.

Paraugaptilus similis A. Scott, 1909 (Figs 27–30)

MATERIAL EXAMINED. ♀ and ♂.

BODY LENGTH. ♀ 3.32 mm; ♂ 3.03 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Figs 27A–C, 28A) asymmetrical, wider than long, swollen anteriorly, widest at level of paired gonopores; each gonopore (Fig. 28B) covered by operculum as in *Arietellus*, anterior half opening; copulatory pores remarkably asymmetrical, right pore located medially on right ventral side, slit-like, approximately 43 µm in length, left pore located ventromedially at about two-thirds distance along double-somite, with round opening, about 27 µm in diameter; both right and left copulatory ducts heavily chitinized; right duct shorter than left, widest near pore opening, constricted medially; left duct thick, with small subchamber medially (see Fig. 27B); seminal receptacles relatively small, right round in shape, left smaller than right, spindle-shaped.

Antennule (Fig. 27D) 20-segmented; seventh (X) to ninth (XII) segments and 11th (XIV) and 12th (XV) segments only partly fused near posterior margin; 20th (XXIII–XXV) and 21st (XXVI–XXVIII) incompletely fused with suture clearly visible. Fusion pattern and armature as follows: I–IV–9 + aesthetasc (I–3, II–2, III–2 + aesthetasc, IV–2), V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2, IX–2, X–2, XI–2 + aesthetasc, XII–2, XIII–2, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–XXVIII–12 + 2 aesthetascs (right), 12 + 3 aesthetascs (left) (XXIII–1, XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–7 + 1 (right) or 2 (left) aesthetascs). First (I–IV) to seventh segments fringed with long setules along posterior margin. Posterior setae on segments XXV and XXVI having thicker setules in right antennule than in left.

Antenna: first endopod segment without inner mid-length seta, second segment (Fig. 29B) about 1.8 times as long as first segment, with 1 inner short seta, and 5 setae and vestigial seta terminally; exopod (Fig. 29A) indistinctly 6-segmented, sixth segment bulbous, unarmed; setal formula 0,1,1,1,1,0. Mandibular palp (Fig. 29C): endopod absent; first exopod segment carrying vestigial seta, fifth segment having 1 normal and 1 reduced seta. Maxillule (Fig. 27E): praecoxal arthrite with 5 spines, 2 of which serrate subterminally, ornamented by minute spinules on both surfaces; coxal endite unarmed; coxal epipodite with 8 setae; basal seta and endopod absent. Maxilla: first praecoxal endite with 1 serrate seta and 1 vestigial element, second endite having single bipinnate seta (Fig. 30A); basal spine (Fig. 29D) with 3 rows of spinules. Maxilliped: fourth and fifth endopod segments (Fig. 27F) each bearing unipinnate innermost seta, sixth segment (Fig. 27G) carrying reduced setae a and b, medium-length serrate seta c whose tip chitinized, and elongate seta d with row of sharp triangular spinules along inner margin.

Leg 1: third exopod segment with 2 outer spines; endopod distinctly 3-segmented. Leg 4: vestigial coxal seta present at inner angle. Leg 5 (Fig. 30B): coxae, intercoxal sclerite, basis

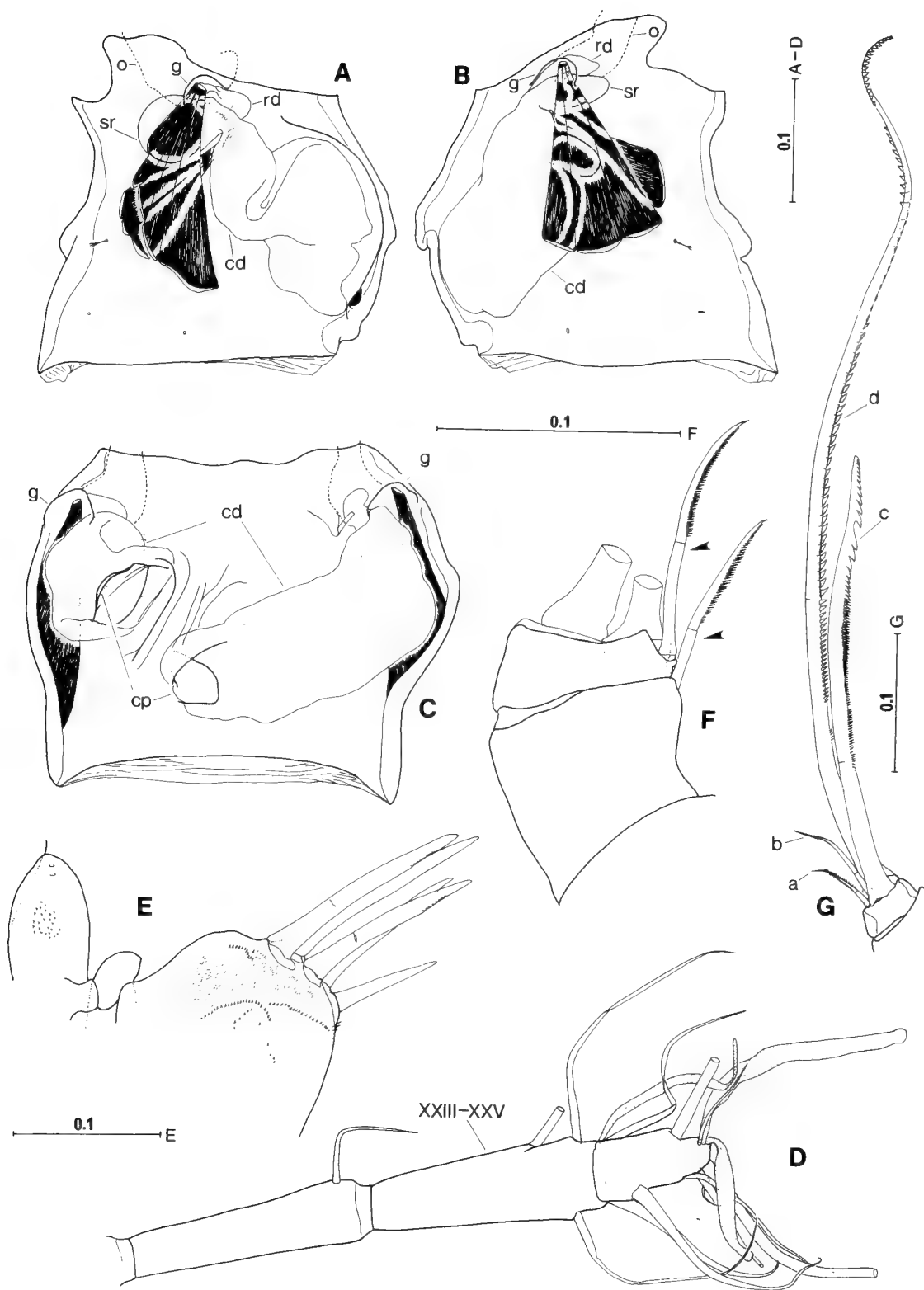


Fig. 27. *Paragaptilus similis*, female. A, Genital double-somite, right lateral view; B, Genital double-somite, left lateral view; C, Genital double-somite, ventral view; D, Antennular segments XXII-XXVIII; E, Praecoxal arthrite, coxal endite and inner margin of basis; F, Fourth and fifth endopod segments of maxilliped, innermost seta indicated by arrowhead, mid-margin seta on fourth segment missing; G, Sixth endopod segment of maxilliped. Scales in mm.

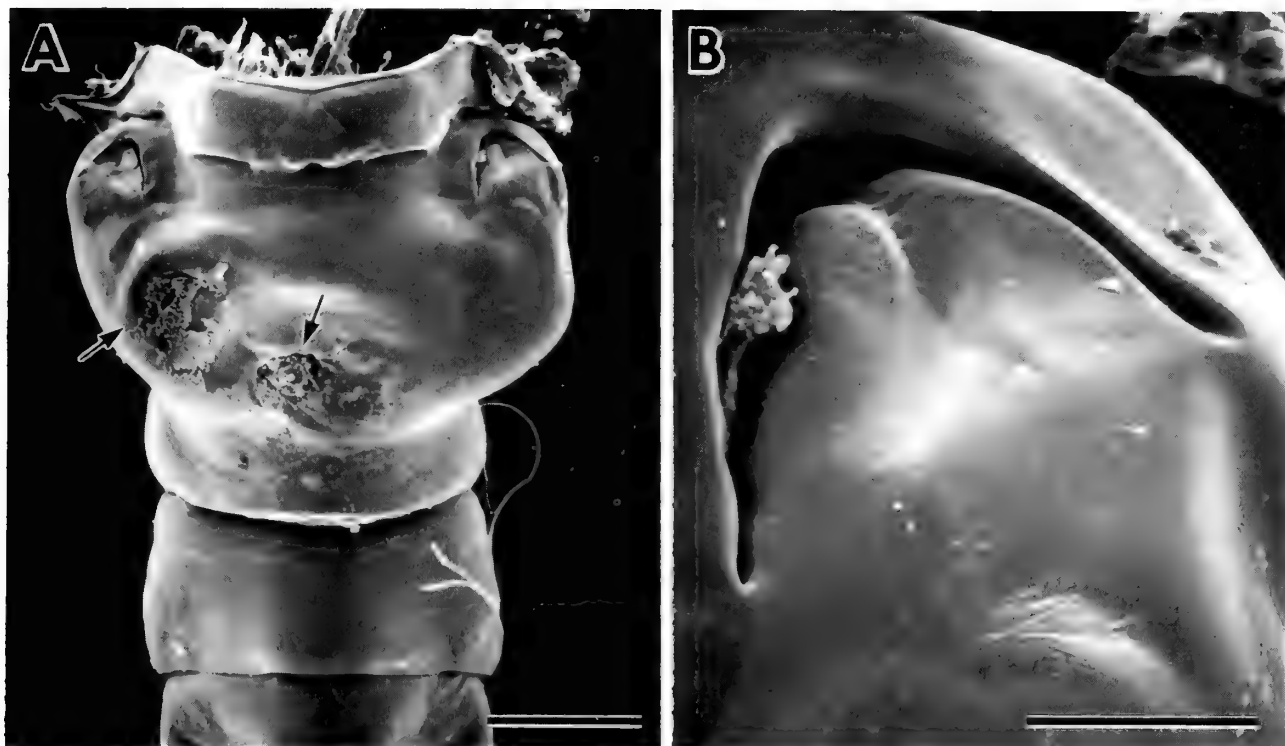


Fig. 28. *Paragaptilus similis*, female. SEM micrographs of genital double-somite. A, Genital double-somite, ventral view, copulatory pores indicated by arrows, scale bar = 100 μ m; B, Left gonopore, scale bar = 20 μ m.

and endopod fused to form flattened plate; basal setae of almost equal length; endopod represented by plumose seta; exopod completely absent.

Male. Left antennule (Fig. 30C-E) 19-segmented; segments IX to XV only partly fused near posterior margin; segments XXI and XXII almost fused, but suture visible near anterior margin; segments XXIV-XXV and XXVI-XXVIII incompletely fused; fusion pattern and armature as follows: I-IV-7 + 4 aesthetascs (I-3 + aesthetasc, II-1 + aesthetasc, III-1 + aesthetasc, IV-2 + aesthetasc), V-2 + aesthetasc, VI-2 + aesthetasc, VII-2 + aesthetasc, VIII-2 + aesthetasc, IX-2 + aesthetasc, X-1 + aesthetasc + process, XI-2 + aesthetasc, XII-1 + aesthetasc + process, XIII-1 + aesthetasc + process, XIV-1 + aesthetasc + process, XV-1 + aesthetasc + process, XVI-2 + aesthetasc, XVII-2 + aesthetasc, XVIII-2 + aesthetasc, XIX-1 + aesthetasc + 2 processes, XX-1 + aesthetasc + process, XXI-XXIII-1 + aesthetasc + 3 processes (XXI-aesthetasc + 2 processes, XXII-process, XXIII-1), XXIV-XXVIII-11 + 2 aesthetascs + process (1 seta missing in Fig. 30E) (XXIV-1 + 1 + process, XXV-1 + 1 + aesthetasc, XXVI-XXVIII-7 + aesthetasc). Only first segment fringed by short setules along posterior margin.

Antenna: second endopod segment (Fig. 29G) approximately 1.3 times as long as first segment, with 1 long and 1 short seta medially; exopod (Fig. 29E,F) indistinctly 7-segmented, terminal compound segment bulbous (IX-X), sixth (VIII) carrying long seta, seventh (IX-X) unarmed. Mandibular palp (Fig. 29H): first exopod segment with long seta.

Leg 5 (Fig. 30F): coxae and intercoxal sclerite almost completely fused; coxa and basis incompletely fused in right leg, but separate in left; right and left endopods consisting of

1 segment. Right exopod 2-segmented, ancestral second and third segments almost completely fused, proximal segment triangular, with short seta at outer angle, distal compound segment lamellar, expanded proximally, tapering distally, carrying short outer seta near base, triangular inner process and 2 patches of setules medially. Left exopod indistinctly 3-segmented, first segment with short seta at outer angle, second swollen inwards, bearing minute setule subterminally, third segment incompletely fused with second segment, having 2 processes, outer bifid at tip, and minute subterminal outer setule.

REMARKS. The large process on segment XXIV of the left antennule probably represents an extension of the cuticular surface rather than a modified setation element. The anterior subterminal process on the counterpart of the male left antennule of *Paragaptiloides magnus* is possibly homologous to that of *Paragaptilus*. The presence of 2 aesthetascs located immediately adjacent to each other on the extreme tip of the left antennule is interpreted here as an abnormality.

Paragaptilus buchani Wolfenden, 1904 (Figs 31,32)

MATERIAL EXAMINED. ♀ and ♂.

BODY LENGTH. ♀ 3.14 mm; ♂ 3.25 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Fig. 31A) similar to that of *P. similis*, but relatively shorter, left copulatory pore located near posterior margin. Female left antennule (Fig. 32A) with same fusion pattern and armature as in female *P. similis* except for following: segment XXIII incom-

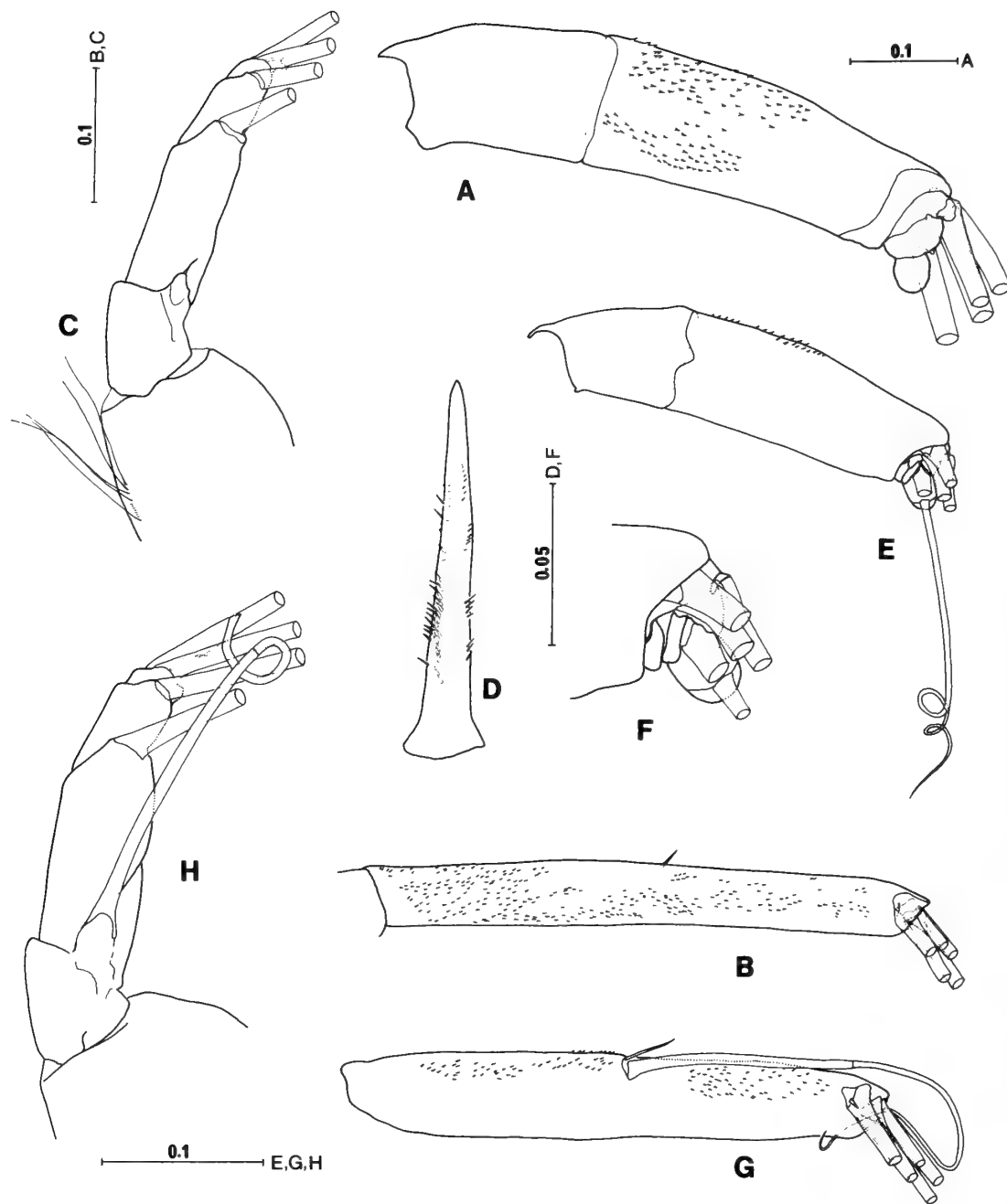


Fig. 29. *Paraugaptilus similis*, female (A-D), male (E-H). A, Antennary exopod; B, Second endopod segment of antenna; C, Mandibular exopod; D, Basal spine of maxilla; E, Antennary exopod; F, Detail of antennary exopod segments IV to X; G, Second endopod segment of antenna; H, Mandibular exopod. Scales in mm.

pletely fused with segments XXIV–XXV; segments XXV and XXVI incompletely fused; left compound segment XXVI–XXVIII with 7 setae and aesthetasc.

Antenna: second endopod segment about 1.9 times as long as first, with 1 minute inner seta at mid-length and 5 setae and 1 vestigial seta terminally, as in *P. similis*; exopod similar in segmentation and setation to that of female *P. similis*. Mandibular palp: first exopod segment with vestigial seta (Fig. 32B) as in female *P. similis*. Maxilliped: sixth endopod segment (Fig. 32E) similar to that of *P. similis*, but seta c with terminal spinules incompletely fused to seta.

Male. Left antennule (Fig. 32F) with same fusion pattern

and armature as in *P. similis* except for following: seta on segment XXII not modified into process; process on segment XXIV–XXV not so developed as in male *P. similis*, not reaching beyond end of antennule, directed straight forwards. Antenna similar in segmentation and setation to that of female; second endopod segment ca. 1.4 times as long as first. Mandibular palp: first exopod segment with well-developed seta (Fig. 32G). Maxillule: praecoxal arthrite (Fig. 32C) with 5 spines; tubular gland opening on inner surface.

Leg 5: both coxae and intercoxal sclerite completely fused as in male *P. similis*; coxa and basis separate in left leg and incompletely fused in right (almost completely fused on

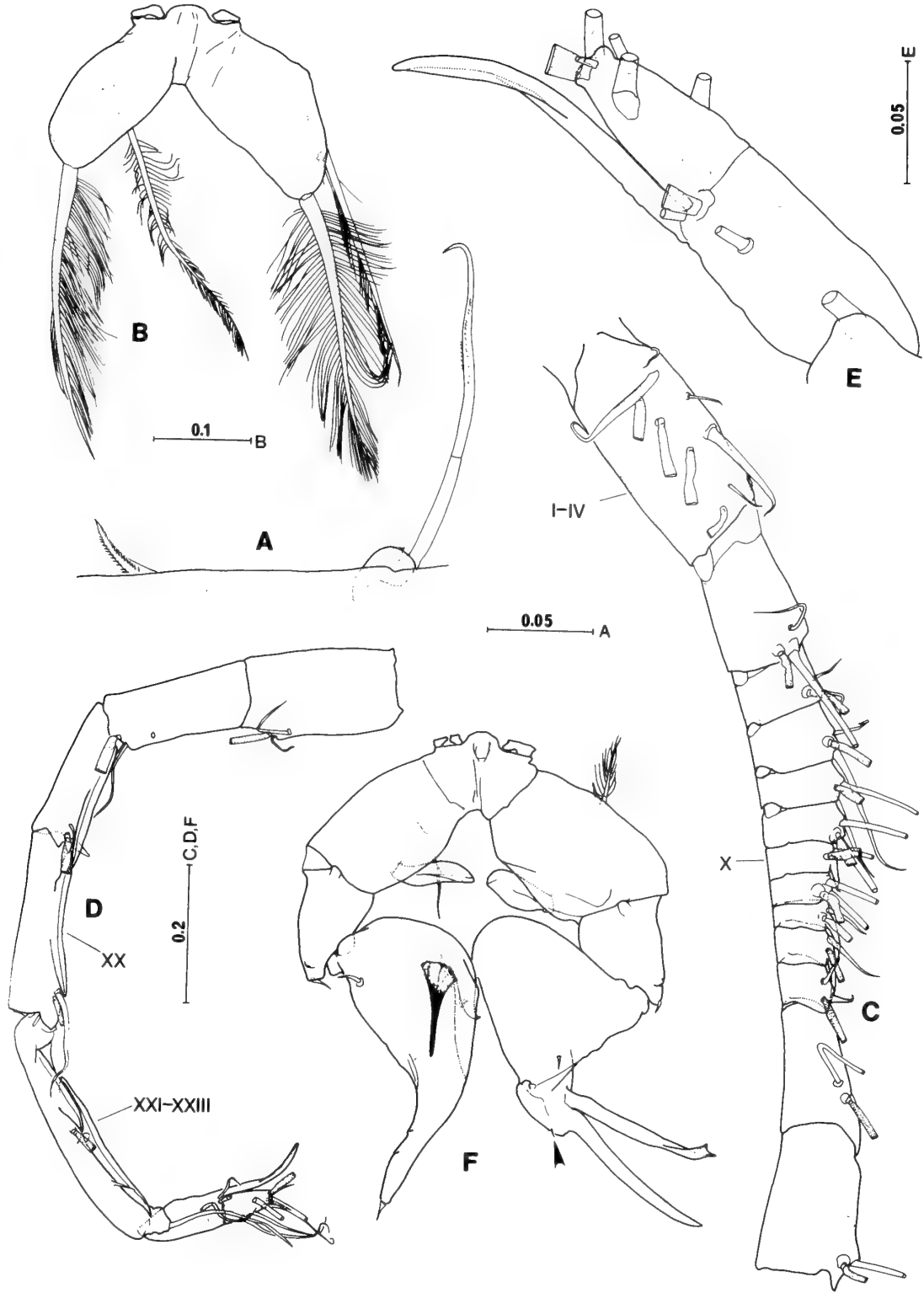


Fig. 30. *Paraugaptilus similis*, female (A,B), male (C-F). A, First and second praecoxal endites of maxilla; B, Leg 5, anterior surface; C, Left antennular segments I to XVI; D, Left antennular segments XVII to XXVIII; E, Left antennular segments XXIV to XXVIII; F, Leg 5, anterior surface, minute seta indicated by arrowhead. Scales in mm.

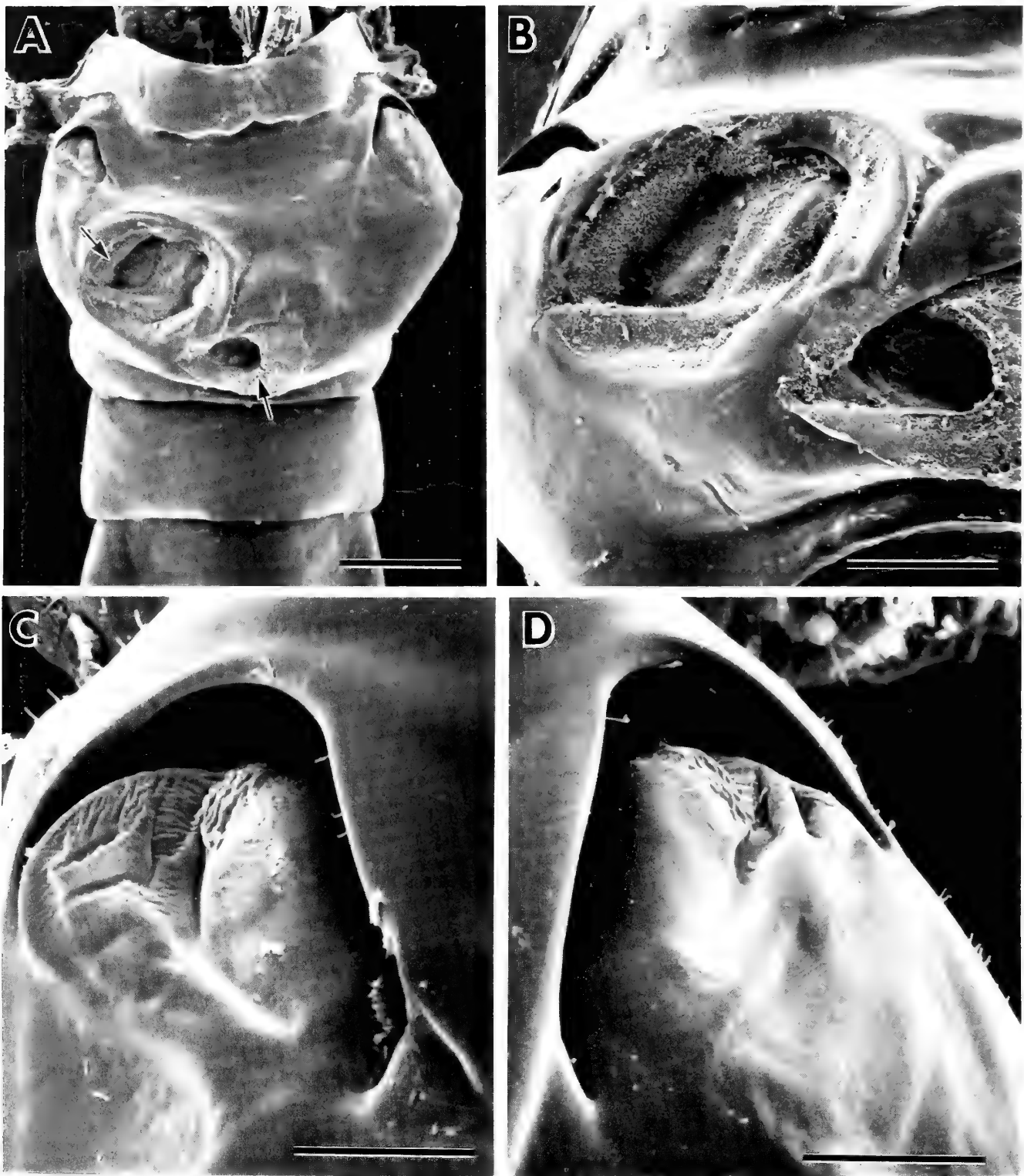


Fig. 31. *Paraugaptilus buchani*, female. SEM micrographs of genital double-somite. A, Genital double-somite, copulatory pores arrowed, scale bar = 100 μm ; B, Copulatory pores, scale bar = 50 μm ; C, Right gonopore, scale bar = 20 μm ; D, Left gonopore, scale bar = 20 μm .

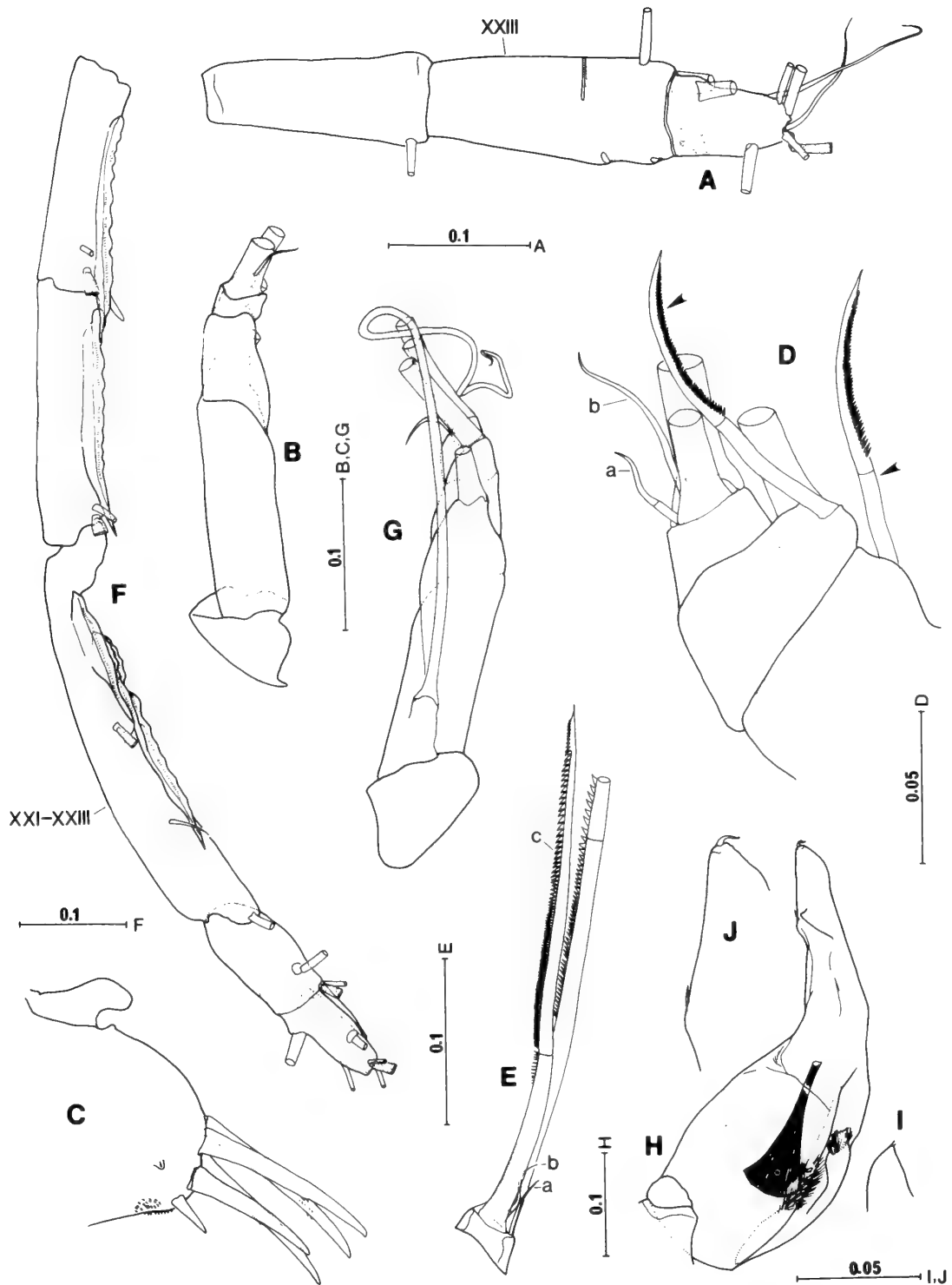


Fig. 32. *Paraugaptilus buchani*, female (A-E), male (F-J). A, Antennular segments XXII to XXVIII; B, Mandibular exopod; C, Praecoxal arthrite and coxal endite of maxillule; D, Fourth to sixth endopod segments of maxilliped, innermost seta on fourth and fifth segments indicated by arrowheads; E, Sixth endopod segment of maxilliped; F, Antennular segments XIX to XXVIII; G, Mandibular exopod; H, Second exopod segment of right leg 5; I, Inner medial process on second exopod segment of right leg 5; J, Outer margin of second exopod segment of right leg 5. Scales in mm.

posterior surface); both endopods 1-segmented, lobate. Right exopod (Fig. 32H-J): second and third segments almost completely fused to form lamelliform compound segment, tapering distally; inner medial triangular process with 2 minute spinules (Fig. 32I) at tip; 1 subterminal outer and 1 terminal setule present (Fig. 32J); muscles between second and third segments present, but less developed than in *Paraugaptiloides*. Left exopod similar to that of male *P. similis*.

REMARKS. Deevey (1973) first discovered sexual dimorphism in the mandibular palp of this species, but overlooked the vestigial seta on the first exopodal segment of the female. *P. buchani* shows no sexual dimorphism in setation of the antennary endopod and exopod, unlike *P. bermudensis* (Deevey, 1973) and *P. similis* (A. Scott, 1909; present study). Unfortunately the only female of *P. buchani* lacked the terminal segments of the right antennule. The posterior setae on segments XXV and XXVI of the left antennule are ornamented with thick setules as in the right antennule of female *P. similis*. In *P. buchani* the asymmetrical pattern in antennular armature elements may be different from that of *P. similis*.

Genus *Scutogerulus* Bradford, 1969

DIAGNOSIS (emended). Only female known. Body relatively large, more than 3 mm long. Cephalosome separate from first pedigerous somite; urosome about one-third as long as prosome. Genital double-somite as long as wide; gonopore and copulatory pore sharing common slit-like aperture, gonopore located anteriorly, copulatory pore at innermost corner of the slit; copulatory duct swollen anteriorly; seminal receptacle relatively small and simple in shape. Caudal rami slightly asymmetrical, left caudal ramus longer than right, longer than wide, with setae II and III relatively long.

Antennules symmetrical, reaching almost to end of prosome, 22-segmented; posterior margin of proximal segments bearing long setules from segment I to XIII; segment III separate from IV; segment IV without aesthetasc; segment XIII with 2 setae; segment XXIII separate from XXIV. Antenna: first endopod segment without inner seta; second endopod segment with 3 medial and 5 terminal setae; exopod indistinctly 8-segmented. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth segment relatively long. Maxillule: praecoxal arthrite with 4 finely serrate spines and 1 process; coxal epipodite with 6 setae; coxal endite carrying 1 long seta; endopod having single seta. Maxilla: first praecoxal endite with 1 relatively well developed seta and 1 vestigial element; second praecoxal endite with 1 seta; basal spine with 3 rows of minute spinules; setae on endopod with row of triangular spinules. Setal formula of endopod of maxilliped: 1,4,4,3,3,4; setae a and b on sixth endopod segment vestigial.

Third exopod segment of leg 1 with outer medial tuft of short setules and subterminal outer spine. Leg 5 biramous, carrying 1-segmented rudimentary endopod with 1 terminal seta and 2-segmented exopod with 1 outer spine on first segment and 2 terminal setae on second segment.

TYPE SPECIES. *Scutogerulus pelophilus* Bradford, 1969 (monotypic).

REMARKS. The new genus *Campaneria* is established for the paratypic male of *S. pelophilus*.

ECOLOGICAL NOTE. Bradford (1969) suggested that *S. pelophilus* is a deep-sea hyperbenthic species. However, Campaner (1984) considered that it was less associated with the bottom than members of his second group, namely, *Paramisophria*, *Rhapidophorus* and some species of *Metacalanus*, since *S. pelophilus* has well-developed antennules and antennae for swimming. The presence of long caudal setae also supports Campaner's (1984) inference.

Scutogerulus pelophilus Bradford, 1969 (Figs 33,34)

MATERIAL EXAMINED. ♀, Paratype, New Zealand Oceanographic Institute, p-121.

BODY LENGTH. 3.6 mm (after Bradford, 1969).

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Urosome (Fig. 33A) slender. Genital double-somite (Fig. 33B,C) as long as wide; paired gonopores and copulatory pores symmetrically arranged; gonopore sharing common slit-like aperture with copulatory pore; gonopore located anteriorly in slit, genital operculum accompanied by muscles; copulatory pore small, located at innermost corner of slit; copulatory duct swollen anteriorly, relatively short; seminal receptacle simple in shape, pea-like; receptacle duct short, opening beneath gonopore. Left caudal ramus slightly longer than right, with seta V longer than urosome (Fig. 33A).

Antennule (Fig. 33D-F): eighth (X) to 10th (XII) segments separate; 12th (XIV) and 13th (XV) segments partly fused (Fig. 33D). Fusion pattern and armature elements as follows: I-III-7 + 2 aesthetascs, IV-2, V-2 + aesthetasc, VI-2 + (small) aesthetasc, VII-2 + aesthetasc, VIII-2 + (small) aesthetasc, IX-2 + aesthetasc, X-2 + (small) aesthetasc, XI-2 + aesthetasc, XII-2 + (small) aesthetasc, XIII-2 + aesthetasc, XIV-2 + aesthetasc, XV-XVI-4 + 2 aesthetasc, XVII-2 + aesthetasc, XVIII-2 + aesthetasc, XIX-2 + aesthetasc, XX-2 + aesthetasc, XXI-2 + aesthetasc, XXII-1, XXIII-1, XXIV-XXV-4 + aesthetasc, XXVI-XXVIII-8 + aesthetasc. First to 11th (XIII) segments fringed with long setules along posterior margin.

Antenna: first endopod segment without inner seta, second segment carrying 3 inner setae and 5 terminal setae; exopod (Fig. 33G) indistinctly 8-segmented, setal formula 0,1,1,1,1,0,3. Mandibular gnathobase missing, probably lost during dissection. Mandibular palp (Fig. 33H): endopod rudimentary, 1-segmented, bearing 2 setae of unequal lengths; seta on first exopod segment not reduced, fifth segment with 2 setae, one of which shorter but not reduced.

Maxillule: praecoxal arthrite (Fig. 34A) with 4 spinulose spines and 1 process along inner margin and row of long setules on surface; coxal endite with well-developed spinulose seta; coxal epipodite with 6 setae (only 4 setae and 2 scars remaining on slide); basal seta short, endopod rudimentary, 1-segmented, with 1 short seta terminally (Fig. 34B). Maxilla (Fig. 34C): first praecoxal endite with spinulose seta and 1 vestigial element, second endite with bilaterally spinulose seta. Maxilliped: innermost seta on fourth and fifth endopod segments (Fig. 34E, indicated by arrowhead) not reduced; sixth endopod segment (Fig. 34F) bearing stout, elongate setae c and d with row of triangular spinules and reduced setae a and b.

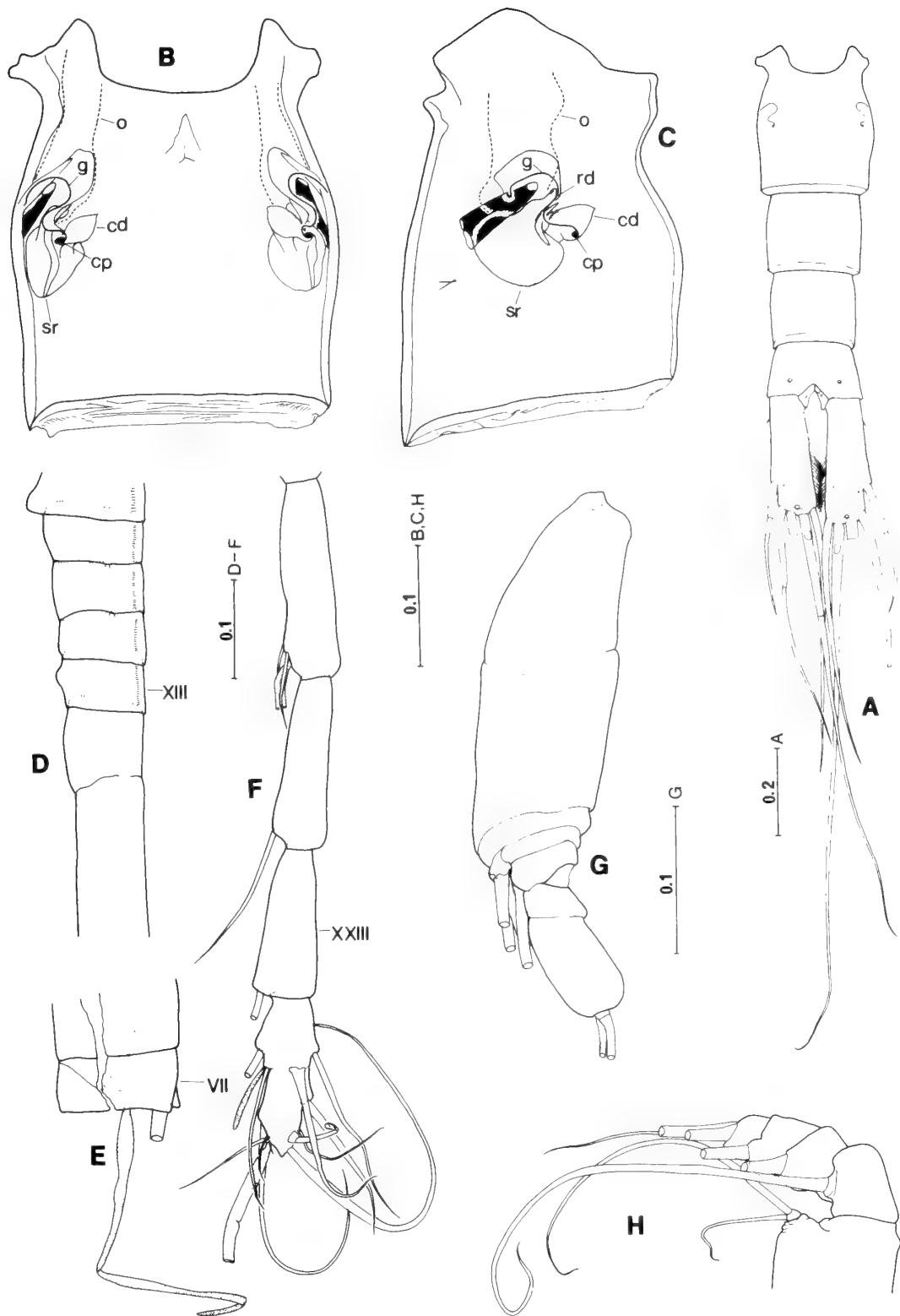


Fig. 33. *Scutogerus pelophilus*, female (paratype). A, Urosome, ventral view; B, Genital double-somite, ventral view; C, Genital double-somite, lateral view; D, Antennular segments IX to XIV, armature omitted; E, Antennular segments VI and VII, note that aesthetasc on each segment differs in size; F, Antennular segments XXI to XXVIII; G, Antennary exopod; H, Mandibular endopod and exopod. Scales in mm.

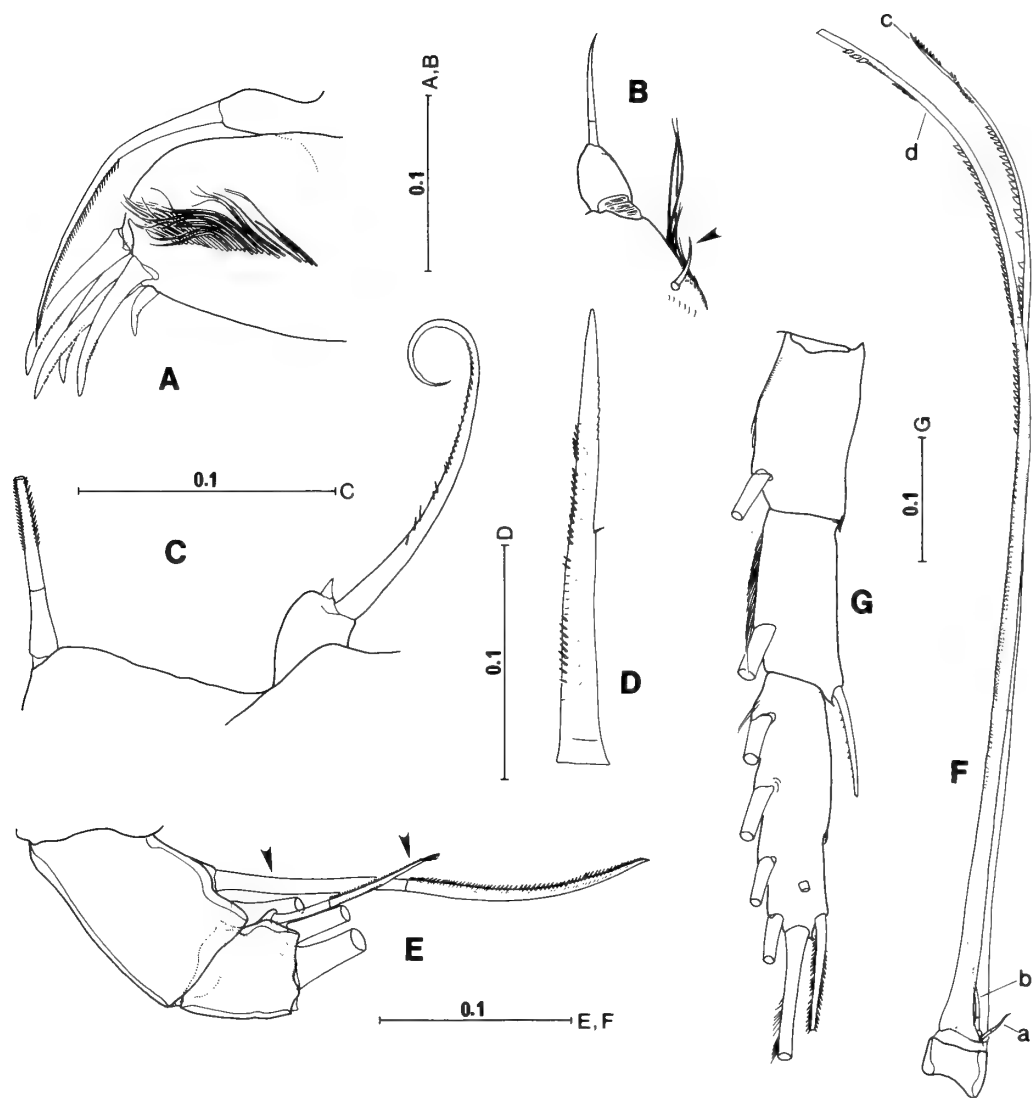


Fig. 34. *Scutogerulus pelophilus*, female (paratype). A, Praecoaxal arthrite and coxal endite of maxillule; B, Maxillulary endopod, basal seta indicated by arrowhead; C, First and second praecoaxal endites of maxilla; D, Basal spine of maxilla; E, Fourth and fifth endopod segments of maxilliped, innermost setae indicated by arrowheads; F, Sixth endopod segment of maxilliped; G, Exopod of leg 1, posterior surface. Scales in mm.

Leg 1 (Fig. 34G): first exopod segment missing element on outer corner, third segment with tuft of minute setules medially and spinulose spine subterminally along outer margin. Leg 5 of paratype missing.

Genus Sarsarietellus Campaner, 1984

DIAGNOSIS (emended). Only female known. Body relatively large, 3 to 5 mm in length. Prosome oblong in dorsal view; cephalosome separate from first pedigerous somite; ventrolateral corner of last prosomal somite slightly produced; urosome about one-third as long as prosome. Genital double-somite longer than wide, produced ventrally; pair of gonopores located anteroventrally, single copulatory pore posteromedially; paired copulatory ducts medially fused to form common duct, heavily chitinized; seminal receptacle elongate, slender, with terminal part bulbous. Caudal rami symmetrical, longer than wide, with setae II and III well developed.

Antennules symmetrical, reaching to end of prosome, 22-segmented; posterior margin of ancestral segments I to X fringed with long setules; segment III separate from IV; segment IV without aesthetasc; segment XIII with 2 setae; segment XXIII separate from XXIV. Antenna: second endopod segment with 5 setae and 1 vestigial seta terminally; exopod indistinctly 8-segmented. Mandibular gnathobase lacking tuft of setules; 3 teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: endopod rudimentary, 1-segmented endopod with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillule: praecoxal arthrite with 6 elements (5 spines and 1 process); coxal epipodite with 8 setae; coxal endite with 1 long seta; endopod bearing 2 setae and 1 vestigial seta. Maxilla: first praecoxal endite with 2 well-developed setae; basal spine with 2 rows of long spinules. Setal formula of endopod segments of maxilliped: 1,4,4,3,3,4; seta a on sixth endopod segment vestigial, seta b relatively long.

Third exopod segment of leg 1 with 2 outer spines. Leg 5: coxa and intercoxal sclerite separate; basis fused to endopod. Endopod represented by process with 2 terminal and 2 inner setae. Exopod composed of 3 almost fused segments, bearing 3 outer spines and 2 terminal spines of unequal lengths.

TYPE SPECIES. *Scottula abyssalis* Sars, 1905.

OTHER SPECIES. *Sarsarietellus natalis* Heinrich, 1993.

REMARKS. Sars (1905) assigned this species to the genus *Scottula* Sars, 1902. *Scottula* was synonymized with the genus *Metacalanus* Cleve, 1901 by Campaner (1984), but he pointed out that *Scottula abyssalis* was not congeneric with *Metacalanus*, and established *Sarsarietellus* to accommodate it. A second species of *Sarsarietellus*, *S. natalis*, has been recently described from the near-bottom (1083–1090 m depth) in the southwestern Indian Ocean (Heinrich, 1993). *S. natalis* exhibits a few more apomorphic characters than *S. abyssalis*: (1) asymmetry in the genital double-somite; (2) reduction of the elements on the exopod of the fifth leg.

ECOLOGICAL NOTE. Campaner (1984) suggested that the genus is only loosely associated with the deep-sea near-bottom as is *Scutogerrulus*. The recent discovery of a second congener from the near-bottom supports his opinion.

Sarsarietellus abyssalis (Sars, 1905) (Figs 35,36)

MATERIAL EXAMINED. ♀, Holotype, Zoological Museum, University of Oslo, Catalog No. F5447–5448.

BODY LENGTH. 3 mm (after Sars, 1925).

DESCRIPTION. Female. Genital double-somite (Fig. 35A,B) longer than wide; its posterior end damaged, but single copulatory pore possibly present posteroventrally (fragment of copulatory pore still remained on slide); anterior paired gonopores located ventro-laterally (since the specimen was dried up, the urosome was so depressed that the internal structures have become artificially asymmetrical); copulatory duct heavily chitinized, divergent anteriorly, each connecting with elongate seminal receptacle (Fig. 35B) which curved anteriorly and reaching to half length of somite with expanded bulbous part terminally.

Antennule (Fig. 36A) 22-segmented; suture between segments XXIV–XXVI visible. Fusion pattern and armature as follows: I–III–7 + aesthetasc, IV–2, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXV–4 + aesthetasc, XXVI–XXVIII–8 + aesthetasc. First to eighth (X) segments fringed with row of setules posteriorly.

Antennary endopod: first segment without inner seta; second segment (Fig. 36B) with 3 setae of unequal lengths medially, and 5 setae and 1 vestigial seta terminally. Antennary exopod (Fig. 36C) indistinctly 8-segmented, first to fifth segments almost fused or incompletely fused, setal formula as follows: 0,1,1,1,1,1,0,3. Mandibular gnathobase with 3 stout teeth, dorsalmost of which bifid at tip, lacking medial tuft of setules as found in *Crassarietellus* sp.; basis fringed by row of long setules along inner margin, and not furnished with minute spinules as in male of *Crassarietellus* sp. Mandibular palp (Fig. 36D): endopod rudimentary, 1-segmented, with 2 setae of unequal lengths; exopod indistinctly 5-segmented, seta on first segment not reduced, outer seta on fifth segment relatively long.

Maxillule (Fig. 36E) praecoxal arthrite with 5 naked spines and 1 process; coxal endite carrying long serrate seta; coxal epipodite with 8 plumose setae; second basal endite bearing 1 vestigial seta; endopod bulbous, 1-segmented, bearing 3 setae, one of which rudimentary. Maxilla: first praecoxal endite (Fig. 36F) with 2 spinulose setae and vestigial element; basal spine (Fig. 36G) stout, bearing 2 rows of long spinules. Maxilliped: fourth endopod segment (Fig. 35C) with relatively developed spinulose innermost seta, fifth segment (Fig. 36D) also having spinulose innermost seta, but much shorter and thinner than on fourth segment; sixth endopod segment (Fig. 36E) with seta a reduced, seta b over half length of medial-length seta c, medium-length spinulose seta c, spinulose seta d elongate.

Leg 4 without inner coxal seta. Leg 5 (Fig. 36H): intercoxal sclerite more or less fused; endopod almost fused with basis, medial suture visible; exopod separate from basis, indistinctly 3-segmented, sutures between segments visible, terminal outer spine almost fused with segment.

REMARKS. Sars (1924, 1925) overlooked the vestigial seta on

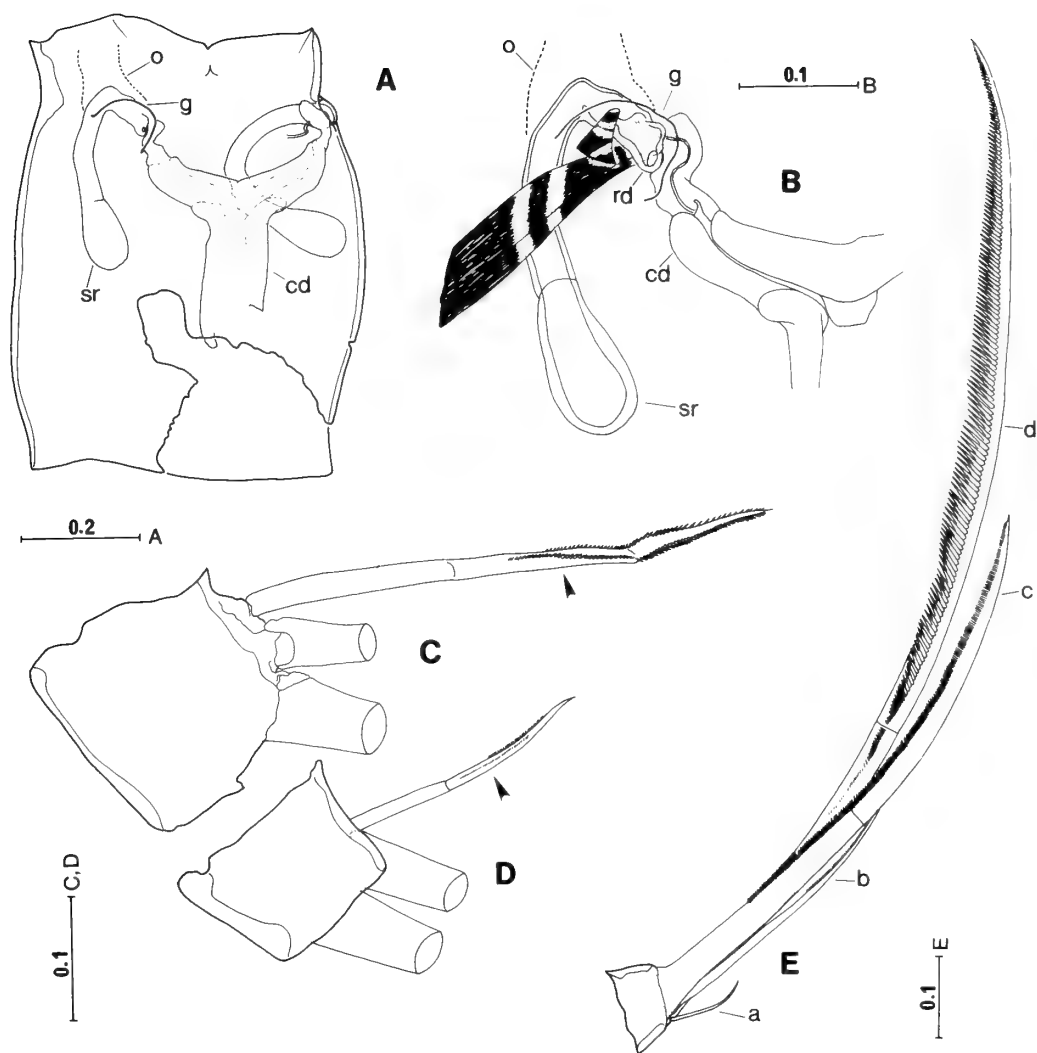


Fig. 35. *Sarsarietellus abyssalis*, female (holotype). A, Genital double-somite, ventral view, part around copulatory pore missing; B, Internal structure of right genital system; C, Fourth endopod segment of maxilliped, innermost seta indicated by arrowhead; D, Fifth endopod segment of maxilliped, innermost seta indicated by arrowhead; E, Sixth endopod segment of maxilliped. Scales in mm.

the second endopodal segment of the antenna, the rudimentary 1-segmented mandibular endopod with 2 setae, and the rudimentary seta on the second basal endite of the maxillule. The terminal segments of the female antennule were re-examined in detail, revealing that there were several misinterpretations of the segmental fusion pattern and of the setation pattern in Sars' (1924, 1925) descriptions.

Genus *Pilarella* Alvarez, 1985

DIAGNOSIS (emended). Only female known. Body relatively small, 1.5 to 1.7 mm in length. Prosome oblong in dorsal view; cephalosome separate from first pedigerous somite; ventrolateral corner of last prosome somite pointed; urosome nearly half as long as prosome. Genital double-somite slightly

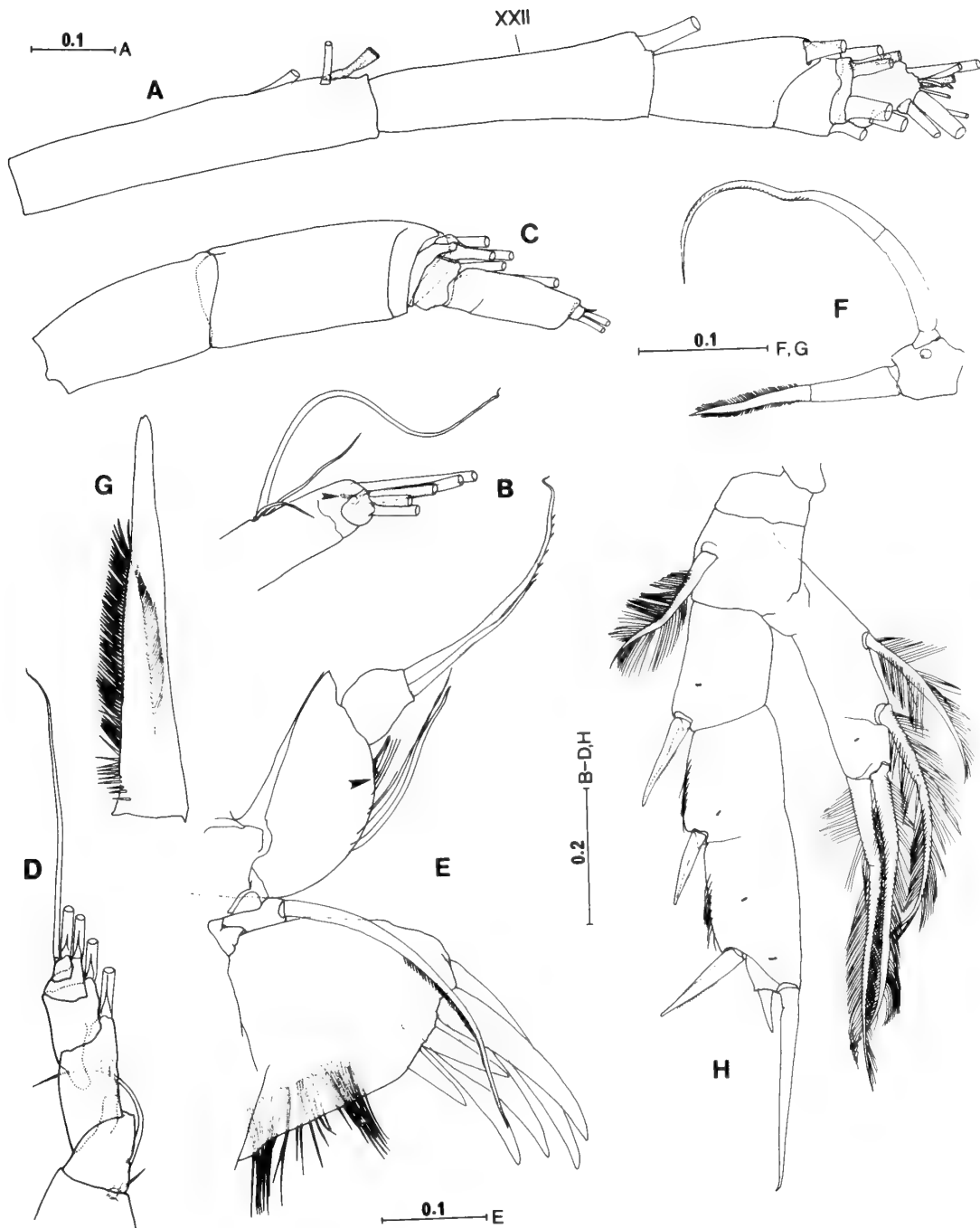


Fig. 36. *Sarsarietellus abyssalis*, female (holotype). A, Antennular segments XXI to XXVIII; B, Terminal part of second endopod segment of antenna, vestigial innermost seta indicated by arrowhead; C, Antennary exopod; D, Mandibular endopod and exopod; E, Praecoxal arthrite, coxal endite, basis and endopod of maxillule, vestigial basal seta indicated by arrowhead; F, First praecoxal endite of maxilla; G, Basal spine of maxilla; H, Leg 5, posterior surface. Scales in mm.

wider than long; entire reproductive system paired, symmetrical; large circular gonopore and small copulatory pore located at outer and inner ends of slit-like aperture, respectively; copulatory duct short, simple; seminal receptacle relatively small, located medial to gonopore. Caudal rami slightly asymmetrical, with right ramus narrower and just shorter than left, with setae II and III relatively long.

Antennules asymmetrical, left longer than right and reach-

ing to end of caudal rami; antennules 21-segmented on both sides; posterior proximal margin lacking long setules; segments I to IV fused, segments IX to XII partially fused; segments XXIV to XXVIII fused into compound apical segment. Antenna: first endopod segment with 1 mid-margin inner seta, second with 3 setae at midlength and 5 setae terminally; exopod indistinctly 7-segmented. Mandibular gnathobase lacking tuft of setules; 4 teeth on cutting edge,

dorsalmost of which tricuspid; endopod rudimentary, 1-segmented with 2 setae; seta on first exopod segment not reduced; outer seta on fifth segment relatively long. Maxillule; praecoxal arthrite with 6 elements (5 setae and 1 process); coxal epipodite with 5 setae; coxal endite with 1 long seta; basal seta absent; endopod bearing 2 setae. Maxilla: first praecoxal endite with 2 setae and vestigial element, second praecoxal endite with 2 setae; basal spine with 2 rows of spinules. Setal formula of endopod segment of maxilliped 1,4,4,4,3,3,4; setae a and b on sixth endopod segment relatively well developed.

Leg 1 with 1 outer spine on third exopod segment. Leg 4 with inner seta on coxa. Leg 5: coxae separate from reduced intercoxal sclerite; endopod represented by 1 seta; exopod and basis separate. Exopod 1-segmented bearing 1 short spine on outer margin and 1 short and 1 long spine terminally.

TYPE SPECIES. *Pilarella longicornis* Alvarez, 1985 (monotypic).

REMARKS. As Alvarez (1985) has already pointed out, the genus *Pilarella* is very similar to *Metacalanus*, but can be distinguished from the latter in the structures of antennules, maxillule and caudal rami. The present study revealed that the genital double-somite of *Pilarella* resembles that of *Scutogasterulus*. A short supplementary description follows, providing details of setation and genital structure that were not apparent in the original description (Alvarez, 1985).

ECOLOGICAL NOTES. The species was collected from near-bottom at a depth of 135 m (Alvarez, 1985), and is, presumably, a shallow-water hyperbenthic species.

Pilarella longicornis Alvarez, 1985 (Fig. 37)

MATERIAL EXAMINED. 3 ♀♀, paratypes, Copepod collection of Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Brasil, No. 186.

BODY LENGTH. 1.53 to 1.73 mm (after Alvarez, 1985).

DESCRIPTION. Genital double-somite (Fig. 37A) wider than long; genital system symmetrical; genital aperture slit-like, located just posterior to mid-length; large circular gonopores present at outermost extremity of genital aperture and small copulatory pore at innermost extremity; copulatory and receptacle ducts short; seminal receptacle relatively small, located medial to gonopore. Caudal rami slightly asymmetrical, with right ramus narrower and just shorter than left, with setae II and III relatively long.

Antennules (see Fig. 39) asymmetrical, left longer than right and reaching to end of caudal rami; both antennules 21-segmented; posterior proximal margin lacking long setules. Fusion pattern and armature as follows: I–IV–9 + 2 aesthetascs, V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs.

Antenna: second endopod segment (Fig. 37B) with 3 setae of unequal lengths at midlength and 5 setae terminally; exopod indistinctly 7-segmented. Maxillule: praecoxal arthrite (Fig. 37C) with 6 elements (5 setae and 1 process); coxal epipodite with 5 setae; endopod bearing 2 setae of unequal

lengths (Fig. 37D). Maxilla: first praecoxal endite with 2 setae and vestigial element (Fig. 37E), second praecoxal endite with 2 spinulose setae; basal spine with 2 rows of spinules. Maxilliped: setae a and b on sixth endopod segment (Fig. 37F) relatively well developed.

Leg 1 with 1 outer spine on third exopod segment. Leg 4 with short inner seta on coxa. Leg 5: coxae separate from small intercoxal sclerite; endopod represented by 1 relatively long seta; exopod and basis separate; exopod 1-segmented bearing 1 short spine on outer middle margin and 1 short outer and 1 long inner spine terminally.

DISCUSSION

Ancestral states and character transformation

All genera of the family Arietellidae except *Rhaphidophorus* are described in detail and their characters are discussed prior to analysis of the phylogenetic relationships between the genera. Within a single genus various states can be observed in appendage segmentation and setation patterns. For example, *Metacalanus* species show a variety of character states in the antennules (Fig. 22) and fifth legs (Fig. 26E,F,H). In such a case, the most plesiomorphic state is selected as the ancestral state for the genus, using the principle of deduction of ancestral states proposed by Huys & Boxshall (1991). Fig. 22 schematically depicts the segmentation and setation of right and left female antennules of 2 new species of *Metacalanus* collected from Okinawa, South Japan. Asymmetry in segmentation and setation is exhibited in both species. The fewest segmental fusions and the greatest number of armature elements on each segment are combined from both antennules of these two species in order to arrive at a hypothetical ancestral condition. The hypothetical antennule of ancestral *Metacalanus* so constructed is used for comparison with antennules of other arietellid genera.

In the antenna and mandibular palp of *Arietellus* and *Paraugaptilus*, which show sexual dimorphism, the more plesiomorphic state from either sex is selected as the generic character state. By reference to the ancestral character states for Calanoida (Huys & Boxshall, 1991) the evolutionary trends within the family are traced.

1. Body plan. The most primitive condition in the family can be seen in *Crassarietellus* and *Sarsarietellus*. The body is symmetrical with complete separation between the cephalosome and the first pedigerous somite; there is no projection at the tip of the cephalosome, no strong dorso- and ventrolateral processes on the last prosomal somite, and no specialization of the caudal ramus.

Asymmetry in the body, except for female genital double-somites, can be seen in the ventrolateral processes on the last prosomal somite in *Arietellus giesbrechti* (Sars, 1924, 1925), *A. mohri* (Björnberg, 1975), and *A. sp.*; in the ventrolateral corners of the second and third pedigerous somites in *Paramisophria giselae* (Campaner, 1977); and in the prosome of *Paramisophria platysoma* (Ohtsuka & Mitsuzumi, 1990). These are more apomorphic states compared with congeners which have symmetrical counterparts. The asymmetrical prosome of *P. platysoma* appears to result from its specialized adaptation to the hyperbenthic zone (Ohtsuka & Mitsuzumi, 1990).

The cephalosome is separate from the first pedigerous

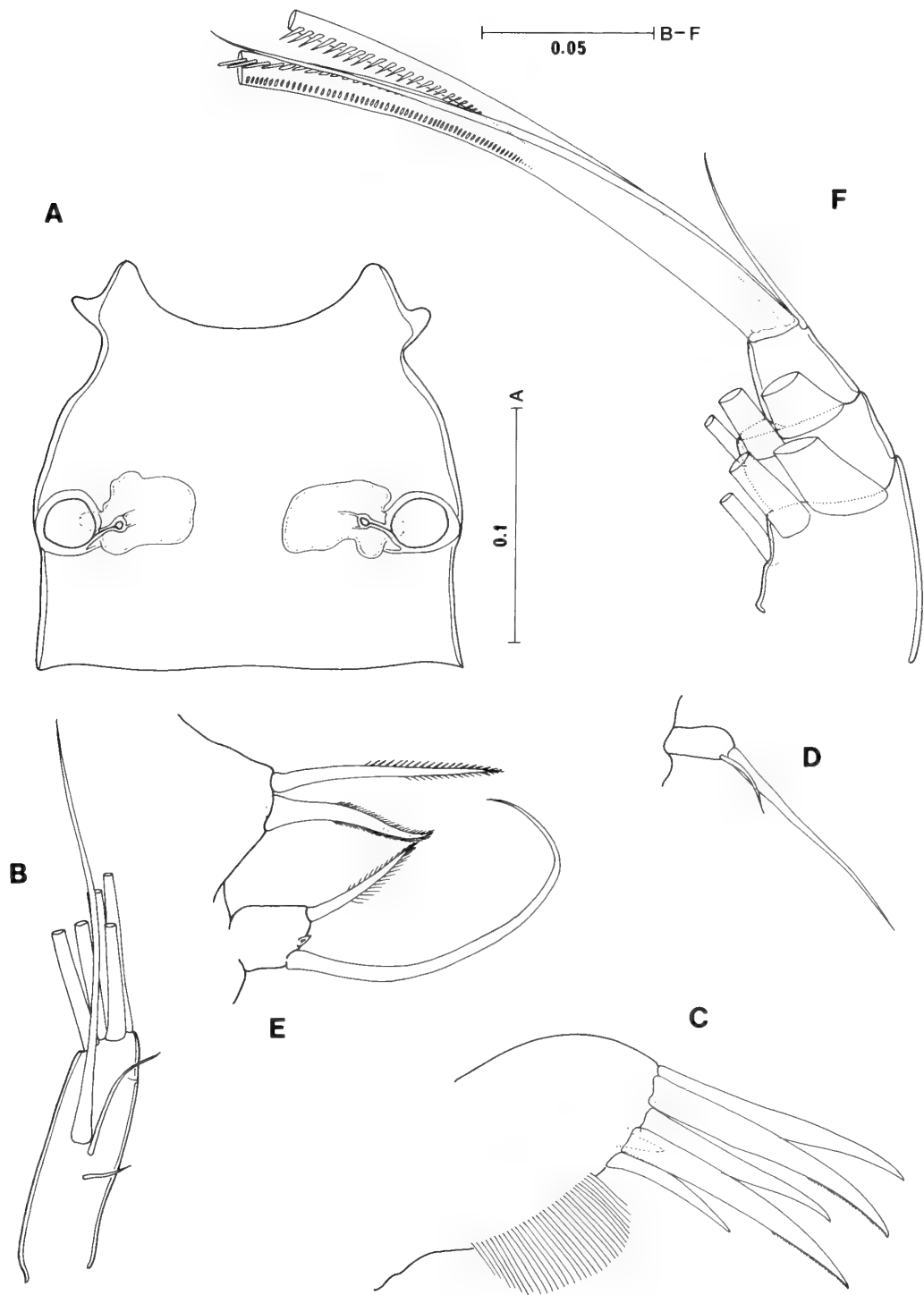


Fig. 37. *Pilarella longicornis*, female (paratype). A, Genital double-somite, ventral view; B, Apical endopod segment of antenna; C, Praecoxal arthrite of maxillule; D, Maxillulary endopod; E, Praecoxal endites of maxilla; F, Tip of endopod of maxilliped showing setae a and b. Scales in mm.

somite in almost all arietellids. Re-examination of those taxa in which the cephalosome and the first pedigerous somite were previously reported to be fused (for example, *Paraugaptilus magnus*), has revealed that these somites are clearly separate. In *Metacalanus* species 1 the cephalosome is weakly fused with the first pedigerous somite ventrolaterally. In all

arietellids the fourth and fifth pedigerous somites are invariably fused, with or without a suture. Within the genus *Arietellus*, *A. setosus* has a well-developed cephalic projection, a pair of strong ventrolateral processes on the last prosomal somite and a posteriorly swollen caudal ramus with remarkably elongate setae. In

contrast *A. simplex* lacks all these characteristics (see Sars, 1924, plates 118, 120). *Paramisophria* species typically have a pair of pointed dorsolateral and rounded or prominent ventrolateral processes on the last prosomal somite (e.g., Sars, 1903; Fosshagen, 1968; Campaner, 1977; McKinnon & Kimmerer, 1985; Ohtsuka, 1985; Ohtsuka & Mitsuzumi, 1990). Although some cave-living species of *Paramisophria* lack such processes (Ohtsuka et al., 1993a), there is a cave-living *Paramisophria* with processes in Bermuda (Fosshagen, personal communication). The genera *Paraugaptilus* and *Paraugaptiloides* consistently exhibit a pair of dorsolateral processes on the last prosomal somite and no cephalic projection (Sars, 1924; Gaudy, 1965; Deevey, 1973; Bradford, 1974). *Sarsarietellus* has weakly developed dorsolateral and/or ventrolateral processes on the last prosomal somite (Sars, 1924, 1925; Heinrich, 1993). *Crassarietellus*, *Metacalanus*, *Scutogerulus*, *Pilarella* and, possibly, *Campaneria* lack dorsolateral processes on the last prosomal somite and a cephalic projection (Bradford, 1969; Alvarez, 1985; present study).

2. Genital double-somite. The present study has revealed an amazing variety of genital systems of arietellid females. The hypothetical ancestral calanoid proposed by Huys & Boxshall (1991) was characterized by paired genital apertures located about in the middle of the genital double-somite. This basic condition is displayed by the genera *Crassarietellus* (Figs 1D,E,2A), *Scutogerulus* (Fig. 33B,C) and *Pilarella* (Fig. 37A). The paired gonopores are ventrolaterally located at about the midlength of the genital double-somite, and the paired copulatory pores are situated either posterior to the gonopores or at the midlength of the somite. *Scutogerulus* exhibits the most plesiomorphic state, similar to that of the primitive family Pseudocyclopidae (see Huys & Boxshall, 1991, Fig. 2.2.32): the gonopore and the copulatory pore share a common opening, with the copulatory pore located on the innermost part of the common opening; the gonopore is located in the outer part of the common opening. Although Huys & Boxshall (1991) did not mention the location of paired seminal receptacles of the ancestor, it is likely that they lie ventrally just beneath the gonopores as proposed for the ancestor of the Cyclopoida (see Huys & Boxshall, 1991, Fig. 2.8.37).

Fig. 38 schematically depicts possible evolutionary trends in structure of the female genital system in the Arietellidae, based on the relative positions of gonopores and copulatory pores. Five major trends are recognizable: (A) fusion of copulatory pores to form a single common pore and anterolateral migration of gonopores; (B) posterior migration of both gonopores and copulatory pores; (C) anterolateral migration of gonopores, and asymmetrical arrangement and enlargement of copulatory pores; (D) lateral migration of both gonopores and copulatory pores, and copulatory pore covered by ventral flap; (E) lateral migration of both gonopores and copulatory pores, copulatory pore uncovered. The first three trends (A-C) are accompanied by the formation of a pair of genital opercula, each of which closes off a gonopore and opens anteriorly with a posterior hinge. The gonopore is separate from the copulatory pore in all except the last trend (E). The first evolutionary trend (A) is exhibited in *Paramisophria*, *Arietellus* and *Sarsarietellus*. The copulatory ducts are heavily chitinized in *Arietellus* and *Sarsarietellus* (see Figs 13B,16A-C) but not so in *Paramisophria* (Figs 19A,20A). In addition, each copulatory duct is connected to a medial part of the seminal receptacle, but not so anteriorly as in *Arietellus*

and *Sarsarietellus*. Even within the genus *Paramisophria*, a remarkable trend is exhibited. In *P. japonica* and *P. reducta*, the copulatory pore is located ventro-medially, whereas in *P. platysoma*, *P. itoi* and *P. cluthae* the pore is present on the left side of the genital double-somite (Ohtsuka & Mitsuzumi, 1990; Huys & Boxshall, 1991; Ohtsuka et al., 1991, 1993b). Alternatively, the copulatory pore can be located on the right side as in *P. giselae*. These asymmetrical species are thought to be more derived than *P. japonica*.

In *Arietellus* the genital system is essentially the same as in *Paramisophria*, but may be relatively more apomorphic in having: (1) copulatory ducts much more heavily chitinized; and (2) enlargement of the copulatory pore. In *Sarsarietellus* the systems are basically similar to those of both *Paramisophria* and *Arietellus*, but are more closely related to *Arietellus* in having the two previously mentioned apomorphic states.

The genus *Metacalanus* exhibits the second trend (B). Primitively, *M. species 2*, *M. inaequicornis* (Campaner, 1984), *M. acutioperculum* (Ohtsuka, 1984), *M. curvirostris* (Ohtsuka, 1985) and, possibly, *M. aurivilli* display paired gonopores and copulatory pores which are located along the posterior margin of the genital double-somite. The gonopores are relatively large. The copulatory pore is clearly separate from the gonopore (see Figs 23A,24A), and is located near the anterior inner corner of the gonopore. The seminal receptacles are located ventrally at almost the same level as the gonopore, and each is connected via a short, chitinized copulatory duct. *M. species 1* shows a further derived state since it completely lacks the genital system on the left side. The right genital structure of this species is quite similar to that of the right side of other *Metacalanus* species, but is bounded by a chitinized flap along the outer lateral margin and the copulatory pore is slightly oblong in shape compared with the rounded pore of the other congeners (see Figs 23,24).

The third trend (C) is exhibited by the genus *Paraugaptilus*. The gonopores are almost symmetrically sited anteriorly (see Figs 28A, 31A) while the copulatory pores are extremely asymmetrical (see Fig. 31B). The right copulatory pore is slit-like and situated in a large circular ventral depression; the left pore is a large pore located posterior to the right. The left copulatory duct is much longer than the right, although both ducts are heavily chitinized. The seminal receptacles are relatively small, bulbous, and located just posterior to the gonopore; the right is better developed than the left (Fig. 27A,B). However, both genital systems are probably functional because of the presence of well-developed muscles which provide an opening-closing mechanism for the genital operculum on both sides. In the recently established calanoid family Hyperbionycidae (Ohtsuka et al., 1993b), only the left genital system is functional; the right side lacks musculature around the gonopore and is probably no longer functional. Only two species of *Paraugaptilus* were available for the present study but Gaudy's (1965) and Deevey's (1973) illustrations of the ventral surfaces of the female genital double-somites of *P. mozambicus* and *P. bermudensis* suggest that these species exhibit the same genital systems.

The fourth (D) and fifth trends (E) are displayed by *Crassarietellus*, and by *Scutogerulus* and *Pilarella*, respectively. Both trends show primitive states of the female genital system in the presence of paired and symmetrically arranged gonopores, copulatory pores and seminal receptacles. However, both trends exhibit different variations of the plesio-

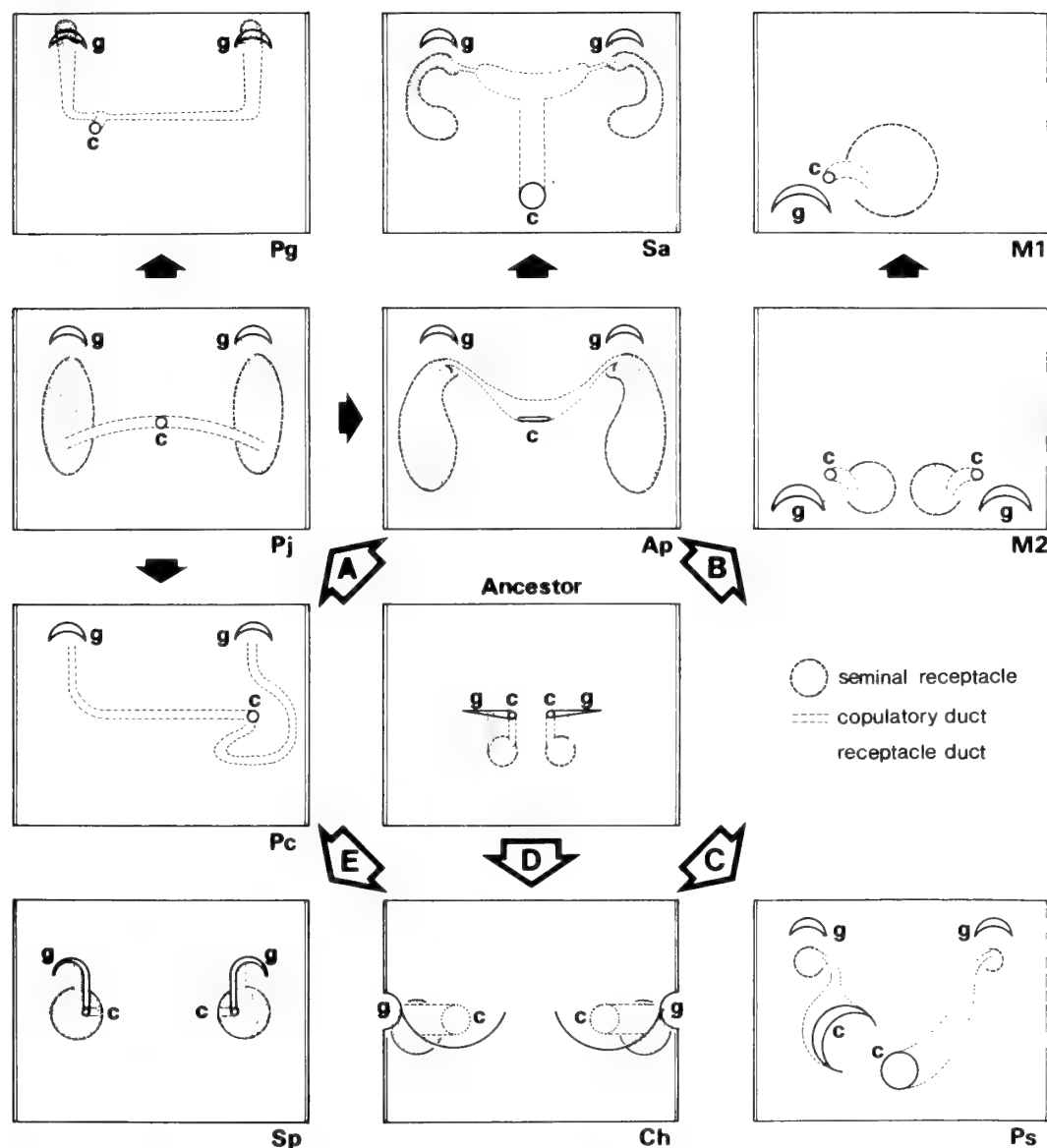


Fig. 38. Evolutionary trends in the structures of the female genital systems of the arietellid genera. A, Fusion of copulatory pores to form single pore, and anterolateral migration of both gonopores; B, Posterior migration of both gonopores and copulatory pores, and separation of copulatory pore from gonopore; C, Anterolateral migration of gonopores, and separation of copulatory pore from gonopore and their asymmetrical arrangement and enlargement; D, Lateral migration of both gonopores and copulatory pores, and separation of copulatory pore from gonopore; E, Lateral migration of both gonopores and copulatory pores. Pg: *Paramisophria giselae*; Pj: *Paramisophria japonica*; Pc: *Paramisophria cluthae*; Sa: *Sarsarietellus abyssalis*; Ap: *Arietellus plumifer*; M1: *Metacalanus* species 1; M2: *Metacalanus* sp. 2; Ps: *Paraugaptilus similis*; Ch: *Crassarietellus huysii*; Sp: *Scutogerulus pelophilus*. g: gonopore; c: copulatory pore.

morphic genital system. In *Scutogerulus* and *Pilarella* each copulatory pore shares a common opening with the gonopore, whereas in *Crassarietellus* each copulatory pore is separate from the gonopore and located beneath the ventral flap. The latter is probably more derived since the copulatory pores are separate from the gonopores. In both trends, the copulatory duct is relatively short and the seminal receptacle is a simple spherical shape.

In the specimens of *Crassarietellus* examined, a pair of fertilization tubes from the spermatophore remnant (Figs 2A,3) was still connected to the copulatory pores. In this genus each copulatory pore seems to be relatively large and opens onto the inner surface of the ventral flap. The end of

the fertilization tube terminates in a mass of brownish opaque material (see Fig. 1E, dotted) positioned where the copulatory pore opens. The gonopore is not covered by a genital operculum, as in other arietellid genera (Fig. 2C,D). An exposed gonopore, as in *Crassarietellus*, is also found in the deep-sea hyperbenthic calanoid family Hyperbionycidae (Ohtsuka et al., 1993b). Owing to the complete absence of armature elements on leg 6 in the Calanoida, it is unknown whether the absence of a genital operculum in *Crassarietellus* represents a secondary loss or a more plesiomorphic state than other arietellids. Radiation of the genital systems of arietellids can be related to their different habitats. Generally, deep-sea hyperbenthic genera such as *Crassarietellus* and

Scutogerulus exhibit a more primitive state than genera found in other habitats, with the exception of *Sarsarietellus* which, however, may be a deep-water hyperbenthic species (Campaner, 1984). In contrast, the shallow-water pelagic and hyperbenthic genera *Metacalanus*, *Paramisophria* and *Pilarella* independently exhibit relatively derived genital systems. The bathypelagic genera *Arietellus* and *Paraugaptilus* have also independently developed a more apomorphic genital system than the deep-sea hyperbenthic genera.

3. Caudal ramus. The caudal rami of almost all arietellids are symmetrical. However, asymmetry of caudal rami is exhibited in *Scutogerulus*, in which the left ramus is slightly longer than the right (Bradford, 1969; present study, Fig. 33A), and in *Pilarella* in which the left caudal ramus is slightly larger than the right (present study).

Except in *Metacalanus* the armature elements on the caudal ramus are all retained. In all genera seta I is minute and setae III–VII are developed to varying degrees. Seta II is relatively minute or completely absent in *Metacalanus*, but always present in the other genera. *Arietellus pavoninus* has highly specialized caudal rami with densely plumose seta II that is directed anteriorly (Sars, 1924, 1925).

4. Rostrum. All arietellids have a well-developed rostrum produced ventrally with a pair of filaments. Both sexes of *Metacalanus curvirostris* have a rostrum that curves to the left (Ohtsuka, 1985).

5. Female antennule. The antennular segmentation and setation patterns of female arietellids are summarized in Fig. 39. Some genera show variability in segmentation and/or setation. In particular, *Metacalanus* exhibits asymmetry in both segmentation and armature (Fig. 22). The segmentation and setation of *Crassarietellus* represent the most plesiomorphic state within the family, displaying both the maximum segmentation and the greatest number of armature elements as follows (Fig. 39A): separation of ancestral segment III from IV; segments IV to XXI each with 2 setae and aesthetasc; segments X–XII separate; segments XIV and XV separate; segments XXIII and XXIV separate.

Ancestral segments I–III are fused in *Crassarietellus* (Fig. 39A), *Scutogerulus* (Fig. 39C), *Sarsarietellus* (Fig. 39B) and *Paramisophria* (Fig. 39D), and segments I–IV in *Arietellus* (Fig. 39E), *Metacalanus* (Fig. 39G), *Paraugaptilus* (Fig. 39F) and *Pilarella* (Fig. 39H). Segments XXIII and XXIV are separate in *Crassarietellus*, *Paramisophria*, *Scutogerulus*, *Sarsarietellus*, *Metacalanus* and *Pilarella*, and fused in *Arietellus* and *Paraugaptilus*. The complete fusion of segments IX and X is unique to *Metacalanus*.

The loss of an aesthetasc on segment IV is found in seven genera; that on segment II in *Pilarella*; that on segment VI in *Arietellus*, *Paraugaptilus*, *Metacalanus* and *Pilarella*; those on segments VIII and X in *Paraugaptilus* and *Metacalanus*; that on segment XII in *Arietellus* and *Paraugaptilus*; those on segments XXII and XXIII in *Pilarella*. One element on segment XIII is reduced in *Paraugaptilus* and *Metacalanus*. One seta on compound segment XXVI–XXVIII is reduced in *Arietellus* and in *Paraugaptilus similis*.

The presence of a duplicated aesthetasc at the extreme tip of antennule of *Paraugaptilus similis* is interpreted here as an individual abnormality.

The right and left antennules are markedly asymmetrical in length in the genera *Paramisophria*, *Metacalanus* and *Pilarella*, which are mainly distributed near the sea bed. This asymmetry has been related to the peculiar swimming behaviour of these genera at the sediment-water interface (see

Ohtsuka & Mitsuzumi, 1990). The ornamentation of the right and left antennules is slightly asymmetrical on the terminal segments in the bathypelagic genus *Paraugaptilus*.

6. Male left antennule. The antennular segmentation and setation patterns of male arietellids are summarized in Fig. 40. Ancestral segments II to IV are incompletely fused in *Campaneria* (Fig. 40A) and completely fused in the other six genera. Fusion of segments IX–X is unique to *Metacalanus* (Fig. 40G), whereas complete separation of segment XXI from XXII is found only in *Campaneria*. Each of ancestral segments II and III carries 2 setae and an aesthetasc in *Crassarietellus* (Fig. 40B), and 1 seta and an aesthetasc in the other genera. In *Arietellus aculeatus* segments I to IV bear 1, 2, 2 and 2 aesthetascs, respectively. The presence of one additional aesthetasc on each segment from II to IV seem to be a secondary addition found in the males of many pelagic calanoids (see Huys & Boxshall, 1991). Huys & Boxshall (1991) speculated that duplication of aesthetascs in males is an adaptation for the open pelagic environment. The oceanic pelagic species *A. aculeatus* shows duplication of aesthetascs, and neither shallow- nor deep-water hyperbenthic arietellids have such duplication. However, no other pelagic species of either *Arietellus* or *Paraugaptilus* has such duplication, and its occurrence within a single species of a relatively derived genus may indicate that the duplication of aesthetascs in *A. aculeatus* arose independently.

A seta on segment XV is modified, by loss of its proximal articulation with the segment, into a process in *Arietellus*, *Paraugaptilus* and *Paraugaptiloides*; a seta on segment XXII is also modified into a process in *Crassarietellus*, *Campaneria* and *Metacalanus*. Only in *Paraugaptilus* and *Paraugaptiloides* does the compound segment XXIV–XXV carry a large distally directed process (Figs 11B, 30E, 32F). From its position, this process may be derived from a setation element of segment XXIV, but we consider it more likely that it represents an outgrowth of the segment. The loss of a seta on the compound segment XXVI–XXVIII is found in *Arietellus* and *Paraugaptilus*. The lack of a seta on segment XIII is unique to *Metacalanus*.

7. Antenna. The ancestral condition of the antennary exopod of Copepoda is shown by Huys & Boxshall (1991): the exopod consists of 10 separate segments; first to ninth segments each bearing a single seta, the 10th segment with 3 setae (Fig. 41A). The segmentation and setation patterns of the arietellid genera are schematically depicted in Fig. 41B–H. In all genera, ancestral exopodal segments I and II, V and VI, VI and VII, and VII and VIII are either completely separate or incompletely fused with a suture still visible. In all genera, ancestral segments IV, V, VI and VII each carry 1 seta while segments I, II, III and IX are unarmed. Segment X carries 3 setae except in *Paraugaptilus* (Fig. 41G,H). A seta is present on segment VIII in *Crassarietellus* (Fig. 41B), *Campaneria* (Fig. 41D), *Paraugaptiloides* (Fig. 41D), *Paramisophria* (Fig. 41D), *Metacalanus* (Fig. 41E), *Sarsarietellus* (Fig. 41D), *Scutogerulus* (Fig. 41D) and *Pilarella* (Fig. 41D), but absent in *Arietellus* (Fig. 41F) and female *Paraugaptilus* (Fig. 41H). Complete fusion of ancestral segments II–IV occurs in *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Metacalanus*, *Paraugaptilus*, *Sarsarietellus*, *Scutogerulus* and *Pilarella*. Complete fusion of segments VIII–IX occurs in *Arietellus*, *Metacalanus* and female *Paraugaptilus*. The most advanced state is found in female *Paraugaptilus* (Fig. 41H): ancestral segments VIII to X are completely fused to form an unarmed, bulbous compound segment in *P.*

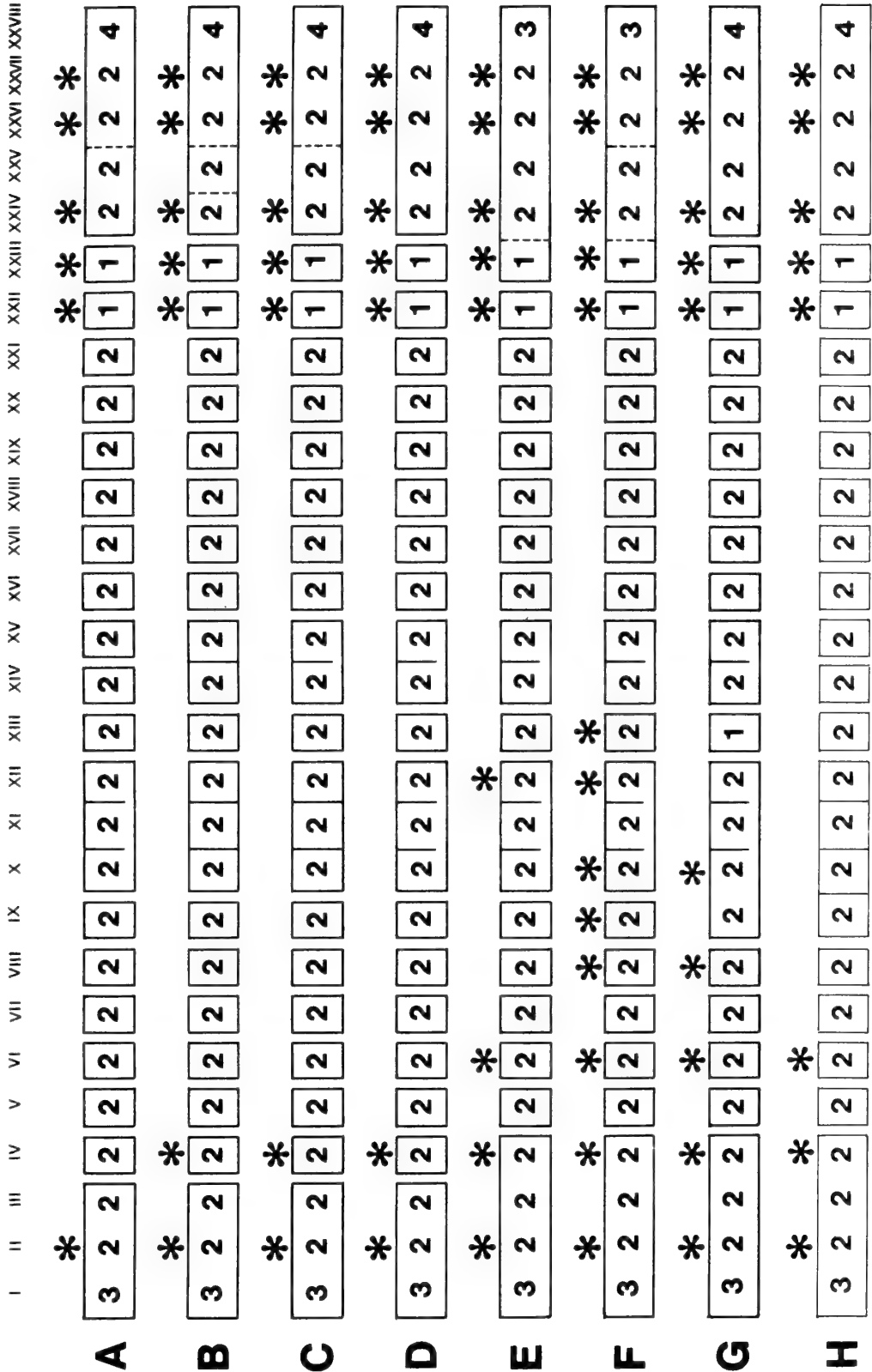


Fig. 39. Schematic illustration of segmental fusion patterns and armature of female antennules of the arietellid genera. A, *Crassarietellus*; B, *Sarsarietellus*; C, *Scutogerrulus*; D, *Paramisophria*; E, *Arietellus*; F, *Paragerrulus*; G, *Metacalanus*; H, *Pilarella*. The number indicates the number of setae on each segment. Asterisk indicates segment without aesthetasc.

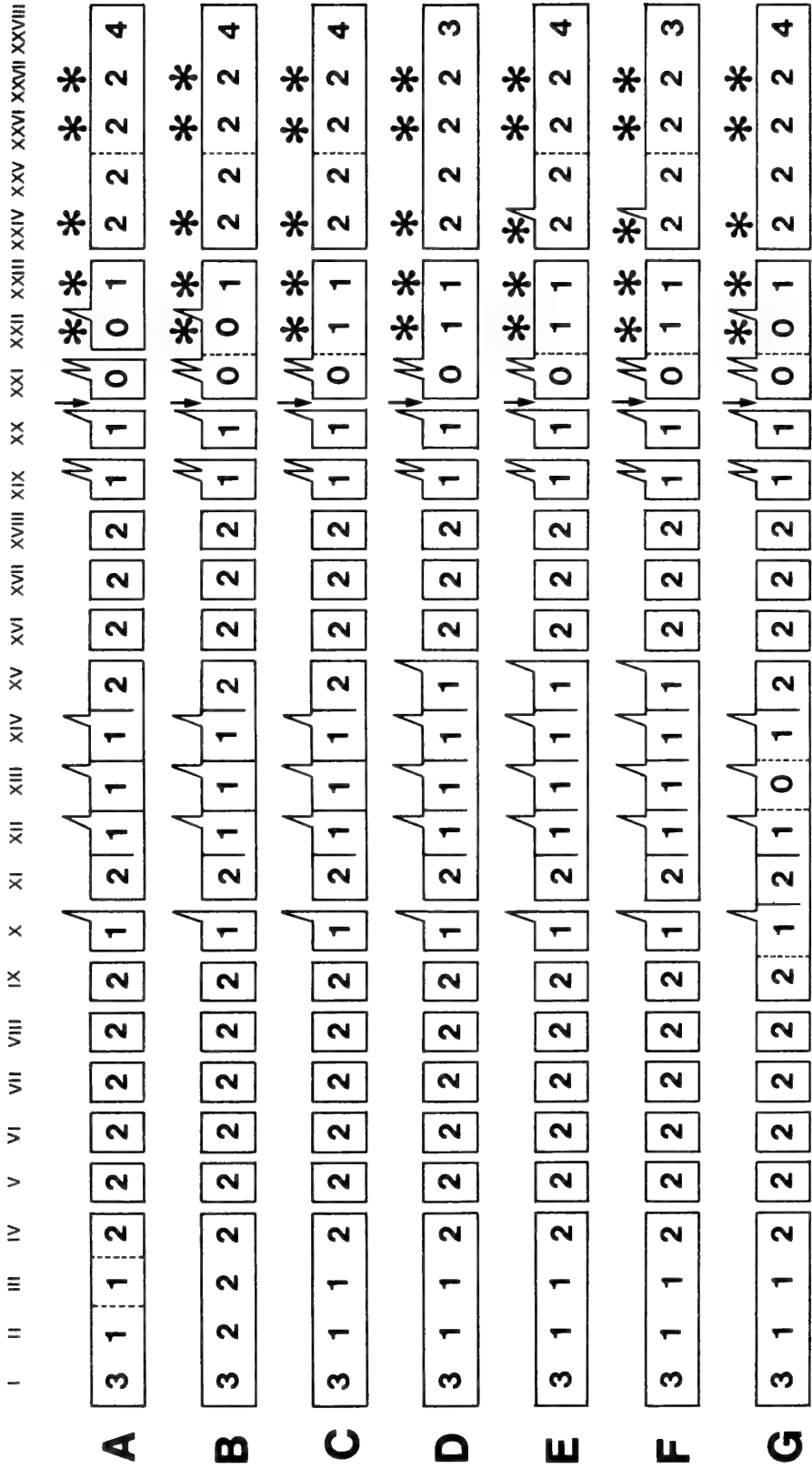


Fig. 40. Schematic illustration of segmental fusion patterns and armature of male antennules of the arietellid genera. A, *Campaneria*; B, *Crassarietellus*; C, *Paramisophria*; D, *Arietellus*; E, *Paraugaptiloides*; F, *Paraugaptilus*; G, *Metacalanus*. The number indicates the number of setae on each segment. Asterisk indicates a segment with no aesthetasc.

similis, *P. buchani*, *P. bermudensis* (Deevey, 1973) and *P. meridionalis* (= *P. buchani* sensu Sars, 1924, 1925). In contrast, males of *P. similis* and *P. bermudensis* are relatively plesiomorphic in that compound segment VIII–X retains a seta which is derived from ancestral segment VIII.

In contrast to the exopodal segmentation, the endopods of arietellids are constantly 2-segmented with the second to fourth ancestral segments almost completely fused. The first segment bears a single minute seta in *Crassarietellus*, *Campaneria*, *Paramisophria*, *Metacalanus* and *Pilarella*, and is unarmed in *Paraugaptiloides*, *Arietellus*, *Paraugaptilus*, *Sarsarietellus* and *Scutogerulus*. The number of inner setae on the second compound segment is variable: 3 in *Crassarietellus*, *Campaneria*, *Paramisophria*, *Sarsarietellus*, *Scutogerulus* and *Pilarella*; 2 in *Paraugaptiloides*, *Arietellus*, *Paraugaptilus* and *Metacalanus* (*Paraugaptilus* has 1 or 2 setae on it). The number of terminal setae on the compound segment is 6 in *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Paraugaptilus* and *Sarsarietellus*, and 5 in *Crassarietellus*, *Campaneria*, *Metacalanus*, *Scutogerulus* and *Pilarella*.

Sexual dimorphism is found in the antennary rami of *Arietellus* and *Paraugaptilus*. The reduction of one of the 2 medial setae on the second endopodal segment of *Arietellus* and some species of *Paraugaptilus* is retained only in the female. In *Paraugaptilus* the relative length of the first and second endopodal segments is different in the sexes. In addition, some species of *Paraugaptilus* (Deevey, 1973; present study) exhibit sexual differences in the exopod in that the ancestral segment VIII is completely fused with segment IX–X in the female and is unarmed, but incompletely fused

with the compound segment and carrying 1 seta in the male. The male shows a more plesiomorphic state in antennary rami than the female.

8. Mandible. Arietellids are typically carnivorous, feeding on copepods and other small organisms (e.g., Ohtsuka & Mitsuzumi, 1990; Ohtsuka et al., 1991). Their mandibular gnathobases are well developed and heavily chitinized, with three or four sharp teeth.

The endopod is either reduced to 1 segment with 1 or 2 setae, or is unarmed and completely fused with the basis. The more plesiomorphic state is retained in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Paramisophria*, *Metacalanus*, *Sarsarietellus*, *Scutogerulus* and *Pilarella*, and the derived state found in *Arietellus* and *Paraugaptilus*.

The first exopodal segment has a normally developed seta in all genera, except for some species of *Arietellus* and *Paraugaptilus*. In these two genera this seta is sexually dimorphic. The males are furnished with a normally developed seta, whereas the females bear a vestigial seta (Sars, 1924; Deevey, 1973; present study). On the fifth exopodal segment, the remarkable reduction of the outer terminal seta is exhibited only by *Arietellus* (Figs 13D, 18B) and *Paraugaptilus* (Fig. 32B).

9. Maxillule. Arietellids exhibit a wide variety of transformed states in the praecoxal arthrite, the coxal endite and epipodite, the basal endite and the endopod. These characters were used to define some arietellid genera by previous authors such as Sars (1903), Rose (1933), Brodsky (1950), Campaner (1977) and Ohtsuka et al. (1993a).

The maximum number of elements on the praecoxal arth-

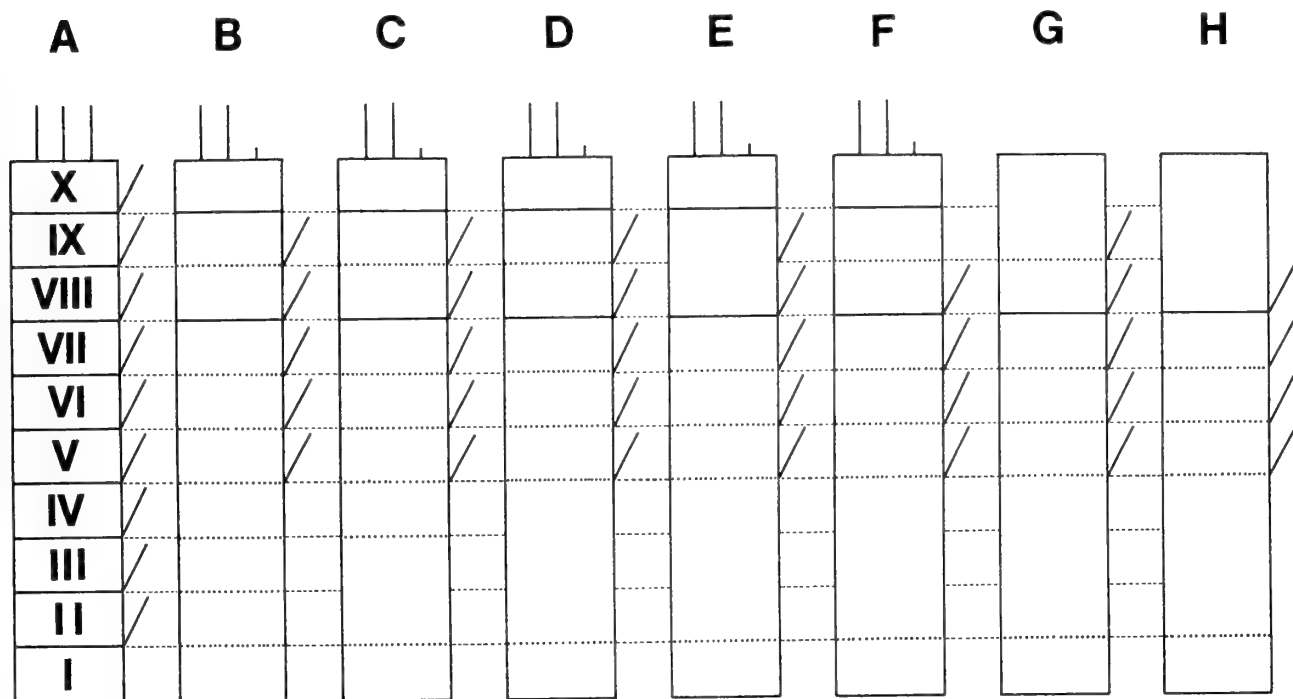


Fig. 41. Schematic illustration of fusion patterns and armature of antennary exopods of the arietellid genera. A, Hypothetical calanoid ancestor; B, *Crassarietellus*; C, *Paramisophria giselae*; D, *Campaneria*, *Paraugaptiloides*, *Paramisophria japonica*, *Sarsarietellus*, *Scutogerulus*; E, *Metacalanus*; F, *Arietellus*; G, *Paraugaptilus similis*, male; H, *P. similis*, female. Solid and dotted lines indicating complete separation between segments, and incomplete fusion or suture between segments, respectively.

rite (5 spines and process) occurs in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Sarsarietellus* and *Pilarella*. In *Sarsarietellus* the outer proximal spine is incompletely fused to the arthrite, while in the other six genera the fusion is complete enough to form a process. Both *Paraugaptilus* (5 spines) and *Scutogerulus* (4 spines and process) show more advanced states, and the reduced element may be the inner proximal spine in both genera. *Metacalanus* exhibits the most apomorphic state, in the number of elements (0–2 setiform spines), and the elements are not so strongly chitinized as in other genera.

On the coxal endite a single seta is present in all the genera except for *Paraugaptilus*. The relative length and the ornamentation of the seta are variable within polytypic genera. The number of setae on the coxal epipodite varies in arietellids. The maximum number (8 setae) is retained in *Paraugaptiloides*, *Arietellus*, *Paraugaptilus* and *Sarsarietellus*, whereas there are 6 in *Crassarietellus* and *Campaneria*, 5 in *Metacalanus*, *Scutogerulus* and *Pilarella*. A vestigial basal seta is present in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Paramisophria* and *Sarsarietellus*, but absent in *Arietellus*, *Metacalanus*, *Paraugaptilus* and *Pilarella*. The position of this seta indicates that it probably represents the second basal endite.

The endopod is variously modified. The most plesiomorphic state, 1-segmented with 3 setae, is found in several species of *Paramisophria*. A 1-segmented endopod with 2 setae is present in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Sarsarietellus* and *Pilarella*; a 1-segmented endopod with a single seta in *Arietellus*, *Metacalanus* and *Scutogerulus*. Species of *Arietellus* and *Metacalanus*, especially the former, exhibit a variety of transformed states in the endopod. The most apomorphic state in these 2 genera is complete incorporation into the basis. Several species of *Arietellus* display an intermediate state with the endopod represented by a rudimentary, unarmed knob, almost fused to the basis. In *Paraugaptilus* the endopod is completely incorporated into the basis.

10. Maxilla. The armature elements on the first and second praecoxal endite, and the ornamentation on the basal and endopodal setae are unique to each genus. On the first praecoxal endite the most primitive state (2 setae and a vestigial element) is retained in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Sarsarietellus*, *Paramisophria* (only *P. giselae*) and *Pilarella*. *Arietellus*, *Metacalanus*, *Paraugaptilus* and *Scutogerulus* share the more apomorphic state (1 seta and a vestigial element). In all these genera it is the outer seta on the endite of the more plesiomorphic genera that is absent and the inner one that remains, based on the position of the setae on the endite.

On the second praecoxal endite, 2 setae are present in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Metacalanus*, *Sarsarietellus* and *Pilarella*, and a single seta in *Paraugaptilus* and *Scutogerulus*. All genera exhibit 2 setae on the first and second coxal endites. The basal spine is variously ornamented in all genera except for *Paramisophria* whose spine is bare. In *Campaneria* (Fig. 10G), *Paraugaptiloides* (Fig. 11F), *Arietellus* (Figs 13I, 18F,G) and *Sarsarietellus* (Fig. 36G), the basal spine is relatively elongate, ornamented with 2 rows of fine, long spinules densely distributed along the entire length except for the bare terminal part. *Crassarietellus* (Figs 5B, 8D) also carries a long basal spine with 2 rows of relatively thick spinules distributed about at midlength. In *Paraugaptilus*

(Fig. 29D) and *Scutogerulus* (Fig. 34D), the spinules are minute and sparsely distributed. *Metacalanus* (Fig. 21I) bears a basal spine unique within arietellids; the spine is relatively short, with 2 rows of minute, rigid spinules at midlength. In *Pilarella* the basal spine is elongate with a single row of spinules at midlength.

The ornamentation on the endopodal setae is also characteristic of each genus. In *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Paramisophria*, *Metacalanus*, *Sarsarietellus* and *Pilarella*, the inner margin of these setae is furnished with a row of slender, simple spinules (see Fig. 11G), whereas in *Arietellus*, *Paraugaptilus* and *Scutogerulus* the ornamentation is variable. *Arietellus* develops a lobate structure basally on each spinule (Fig. 15B,C), while both *Paraugaptilus* (Fig. 27G) and *Scutogerulus* (Fig. 34F) carry a row of triangular spinules along the inner margin of each seta. In arietellids such setal ornamentation on the maxilla is also found on the well-developed setae of the terminal endopod segments of the maxilliped. Bradford (1969) referred to the setal ornamentation on the maxilla and maxilliped of *Scutogerulus* as 'shield-shaped appendages' in her definition of the genus.

11. Maxilliped. Variation in arietellids can be found in the armature on the fourth to sixth endopodal segments. The innermost seta on the fourth and fifth segments is relatively well-developed in all the genera except for *Arietellus*, in which it is reduced to a vestigial element or is completely absent. In *Crassarietellus* (Figs 6B,C, 8E), *Metacalanus* (Fig. 26A,B), *Paramisophria* (Fig. 19D), *Paraugaptilus* (Fig. 27F) and *Pilarella*, the innermost setae on the fourth and fifth endopodal segments are of almost equal length; in *Campaneria* (Fig. 10H), *Paraugaptiloides* (Fig. 12B), *Sarsarietellus* (Fig. 35C,D) and *Scutogerulus* (Fig. 34E) the innermost seta on the fourth endopodal segment is longer than that on the fifth.

On the sixth endopodal segment the most plesiomorphic state, with setae a and b developed, is retained in *Crassarietellus* (Fig. 5C), *Paramisophria* (Fig. 19E), *Metacalanus* (Fig. 26C) and *Pilarella* (Fig. 37F); the most apomorphic state, namely, reduced setae a and b is found in *Arietellus* (Fig. 18H–K), *Paraugaptilus* (Fig. 27G) and *Scutogerulus* (Fig. 34F). *Campaneria* (Fig. 10I), *Paraugaptiloides* (Fig. 12B) and *Sarsarietellus* (Fig. 35E) show an intermediate condition: only seta a is reduced and seta b is relatively long. In *Paraugaptilus* only seta c is specialized, with its terminal part heavily chitinized and serrated along the inner margin (Figs 27G, 32E). *Paraugaptiloides*, however, shows no specialization of seta c (Fig. 12B).

12. Leg 1. On the third exopodal segment two outer spines are retained in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Paraugaptilus* and *Sarsarietellus*. A single outer spine is found in *Metacalanus*, *Scutogerulus* and *Pilarella*. Consideration of the relative position of the spines suggests that it is the proximal spine that is lost in these three genera.

13. Legs 2 and 3. All genera and species, except for the cave-dwelling *Paramisophria galapagensis*, retained the maximum setation of the endopods of legs 2 and 3: seta and spine formula 0–1;0–2;2,2,4. In *P. galapagensis* the seta and spine formula of the endopod is 0–1;0–2;2,2,3 (Ohtsuka et al., 1993a). This represents the most apomorphic state known in arietellids.

14. Leg 4. An inner coxal seta or a vestigial element is present only in *Paraugaptiloides*, *Paraugaptilus* and *Pilarella*. It is absent in the other genera, although a fourth copepodid

stage of *Paramisophria* sp. collected from South Japan carries a minute inner coxal seta (Ohtsuka et al., 1991, Fig. 6J,K). The maximum setation on the third endopodal segment is retained in all the genera and species except for *P. galapagensis*: 2,2,2 in *P. galapagensis* and 2,2,3 in other taxa (Ohtsuka et al., 1993a).

15. Female leg 5. The female fifth legs of arietellids are variable, as in several other calanoid families and the misophrioid family Misophriidae by Huys & Boxshall (1991). Campaner (1984) compared the structure of leg 5 in both sexes but drew no strict homologies of segmentation and armature elements.

Fig. 42 schematically depicts apparent evolutionary trends in the structure of female leg 5 within the genera *Arietellus*, *Paraugaptilus*, *Paramisophria*, *Metacalanus* and *Pilarella*. Within the genus *Arietellus*, three obvious evolutionary trends in segmentation and setation can be recognized: incorporation of the endopod into the basis, reduction of endopodal setae, and fusion of coxa, basis and both rami. The genus *Paramisophria* also exhibits two distinct evolutionary trends: reduction in numbers of endopodal setae and of exopodal spines. In the genus *Metacalanus* reduction of the endopod, and fusion of both rami into the basis plus reduction in number of elements on the exopod occur. Based on these evolutionary trends, the derivation of the *Paraugaptilus* state from an *Arietellus*-like condition, the relationships between *Sarsarietellus* and *Paramisophria* spp., and the derivation of *Metacalanus* from a *Paramisophria*-like ancestor, as already proposed by Campaner (1984), are supported. The setation of *Crassarietellus* (Fig. 6K,L) suggests a close relationship with *Paramisophria*, especially in the endopod setation.

Consideration of the plesiomorphic states exhibited in leg 5 of all female arietellids indicates that the hypothetical ancestor may be characterized by having retained a) the coxa, the basis and 3-segmented exopod and 2-segmented endopod as separate segments; b) basal seta present; c) intercoxal sclerite separate from coxae; d) setal formula of endopod segments 0-2;0,1,1; and e) setal formula of exopod I-0;I-0;II,I,0.

In *Crassarietellus* and *Scutogerulus* the endopod is distinctly separate from the basis, is 1-segmented, and bears 2 and 1 setae respectively. In *Arietellus*, *Paramisophria*, *Metacalanus*, *Paraugaptilus*, *Sarsarietellus* and *Pilarella* the endopod is completely or incompletely fused with the basis, and is represented by 0-4 setae. In *Paramisophria* the number of setae on the endopod ranges from 0 to 2; in *Arietellus* from 1 to 3 setae. In *Metacalanus*, *Paraugaptilus* and *Pilarella* the endopod is represented by 0-1 seta, and is almost completely incorporated into the basis.

In *P. japonica* (Ohtsuka et al., 1991, Fig. 3F,G) and *Scutogerulus* (Bradford, 1969, Fig. 181) the exopod is composed of 2 distinct segments. Particularly in *P. japonica* the ancestral second and third exopodal segments are incompletely fused with a suture visible on the anterior surface. In *Crassarietellus* (Fig. 6K,L) and *Sarsarietellus* (Fig. 36H) the first to third exopodal segments are almost fused with a suture just visible. In *Arietellus* (except for *A. mohri* and *A. sp.*), almost all species of *Paramisophria* (except for *P. giselae*), *Metacalanus* (except for *M. aurivilli* and *M. acutioperculum*) and *Pilarella*, the exopod is distinctly 1-segmented, but variably armed. *Arietellus* carries only a single terminal spine; *Paramisophria* bearing 2 or 3 lateral and 2 terminal spines; *Metacalanus* has 1 terminal spine or 2 terminal and 1 lateral spine. The unarmed exopods of *A. mohri* and *A. sp.*

are lobate and almost completely fused with the basis. In *M. aurivilli* and *M. acutioperculum* the exopod is represented by a small knob with a single terminal seta. In *Paraugaptilus* the exopod is completely incorporated into the basis.

The intercoxal sclerite and coxa are completely separate in *Sarsarietellus*, *Metacalanus*, *Pilarella* and *P. giselae*, and incompletely in *Crassarietellus* and *Arietellus* (except for *A. mohri* and *A. sp.*). In *Paramisophria* (except for *P. giselae*), *Paraugaptilus*, *A. mohri* and *A. sp.* fusion is almost or completely accomplished.

Little attention was paid to the variability within a genus by Campaner (1984). Within genera such as *Arietellus*, *Paramisophria* and *Metacalanus*, the reduction in segmentation and setation is more variable than expected. Reductions in segmentation and setation appear to occur independently within each genus. For instance, the fusion between coxa and intercoxal sclerite probably evolved independently in *Arietellus* (see Fig. 17) and *Paramisophria* (Fig. 20E,F). The number of elements on both rami vary widely in these genera, whereas the outer basal seta is consistently present in all genera and species. In *Arietellus* the right basal seta is slightly or considerably longer than the left.

16. Male leg 5. Campaner (1984) showed a possible relationship between the male fifth legs of arietellids, based mainly on the presence or absence of the endopod on either side. However, the homologies of segmentation and setation were not considered in detail. Compared with the female fifth legs, the male legs are less variable in segmentation and setation within a genus. A scheme indicating possible derivations of segmentation and setation is given in Fig. 43.

The hypothetical ancestral state is based on all taxa and consists of a) intercoxal sclerite and coxa separate; b) coxa completely separate from basis; c) basal seta present; d) 2-segmented, unarmed left endopod; e) 1-segmented, unarmed right endopod; f) 3-segmented right and left exopods; and g) setal formula I-0;I-1;III,I,0. The presence of a basal seta and the numbers of first and second exopodal elements are constant in all genera.

Although the left endopod of *Paramisophria japonica* (Ohtsuka et al., 1991, Fig. 4K) and the right endopod of *Paraugaptiloides* (Fig. 12E) each bear a minute terminal spinule, we are not certain whether it is homologous with a true setation element.

In *Campaneria*, *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*, both right and left endopods are present. In the first three genera a distinctly or indistinctly 2-segmented left endopod is present, while the right endopods of all four genera comprise a single segment. In *Paraugaptiloides* the first and second endopodal segments are completely separate and are accompanied by musculature, indicating that the articulation between these segments is functional. In *Crassarietellus* and *Paramisophria* (except for *P. cluthae*) only the left endopod is retained and the right endopod is absent; the former has an indistinctly 2-segmented left endopod while in the latter this ramus is 1-segmented. In *Metacalanus* both right and left endopods are completely absent.

The most plesiomorphic state in segmentation and armature of the exopod is retained in *Paramisophria*: in both legs, the third segment is separate from the second (cf. Fosshagen, 1968) and 4 elements are present on the third segment of both legs (see Ohtsuka & Mitsuzumi, 1990, Fig. 4E,F). In *Crassarietellus* and *Paraugaptiloides* a vestigial outer proximal element is present on the left third exopod segment, which carries 4 elements in total. The number of elements on the

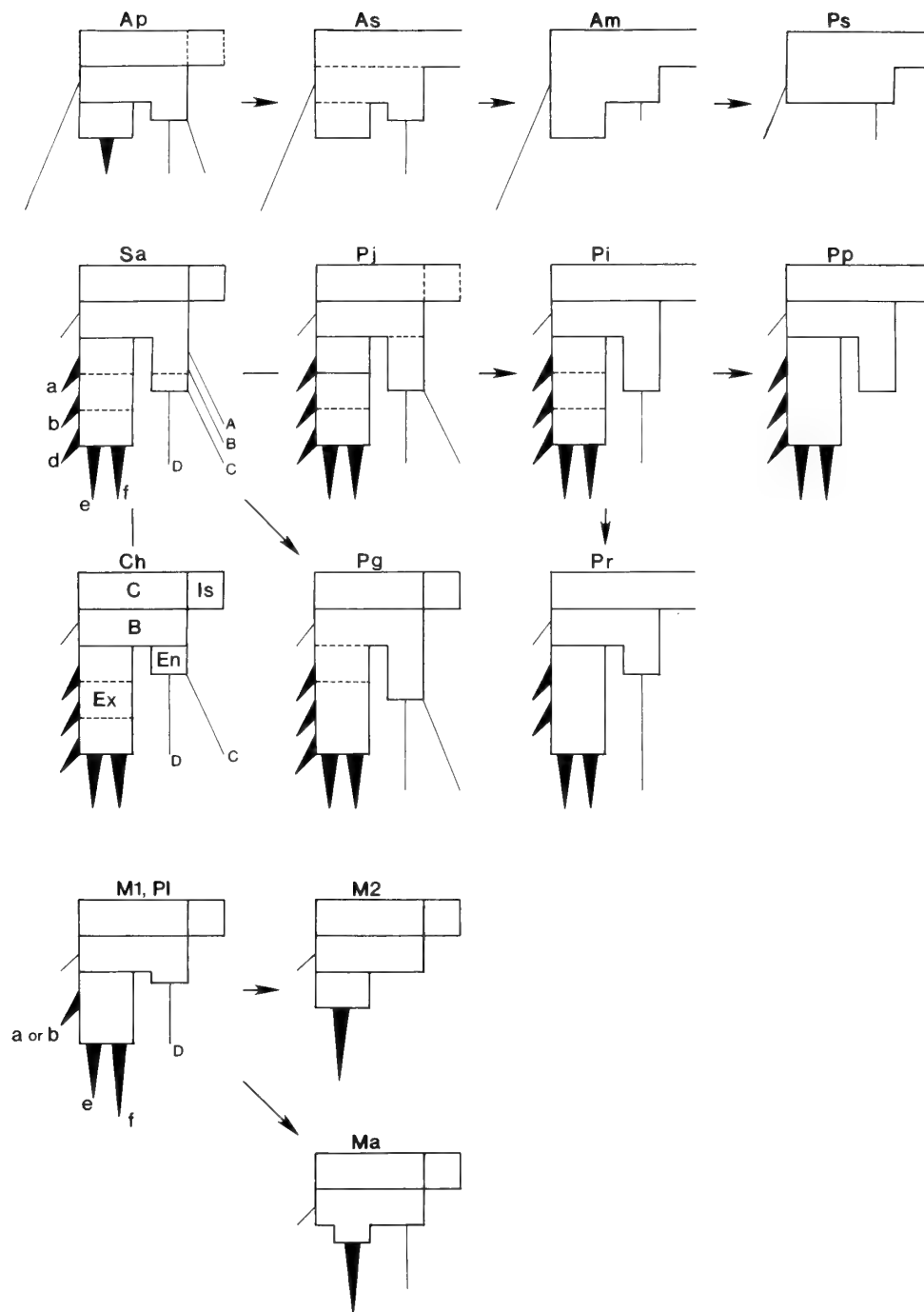


Fig. 42. Schematic comparison of patterns of segmentation and setation of female fifth legs in some arietellids. The arrows indicate possible derivations of setation and segmentation patterns and are not indicative of ancestor-descendant relationships between taxa. Ap: *Arietellus pavoninus*; As: *A. sp.*; Am: *A. mohri*; Ps: *Paraugaptilus similis*; Sa: *Sarsarietellus abyssalis*; Pj: *Paramisophria japonica*; Pi: *P. itoi*; Pp: *P. platysoma*; Pg: *P. giselae*; Pr: *P. reducta*; Ch: *Crassarietellus huysi*; M1: *Metacalanus* species 1; M2: *M. species 2*; Ma: *M. acutioperculum*; Pl: *Pilarella longicornis*. C: Coxa; B (in Ch): Basis; Is: Intercoxal sclerite; Ex: Exopod; En: Endopod. A-D (in Sa): setae on endopod; a-f: spines on exopod.

third exopod segment of the right leg is 3 in *Campaneria*, 2 in *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*, and 1 in *Metacalanus*; on the left leg it is 3 in *Campaneria* and *Arietellus* and 1 in *Metacalanus*. The distal two exopodal segments are separate in both legs in *Paraugaptiloides*, *Paramisophria* and *Metacalanus*, and fused in both legs of *Campaneria* and

Paraugaptilus and in the right leg only in *Arietellus*. The distal two segments of the right leg are missing in the only known male of *Crassarietellus* sp. The terminal and subterminal elements on the third exopodal segment of the left leg are heavily chitinized and almost fused to the segment only in *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*.

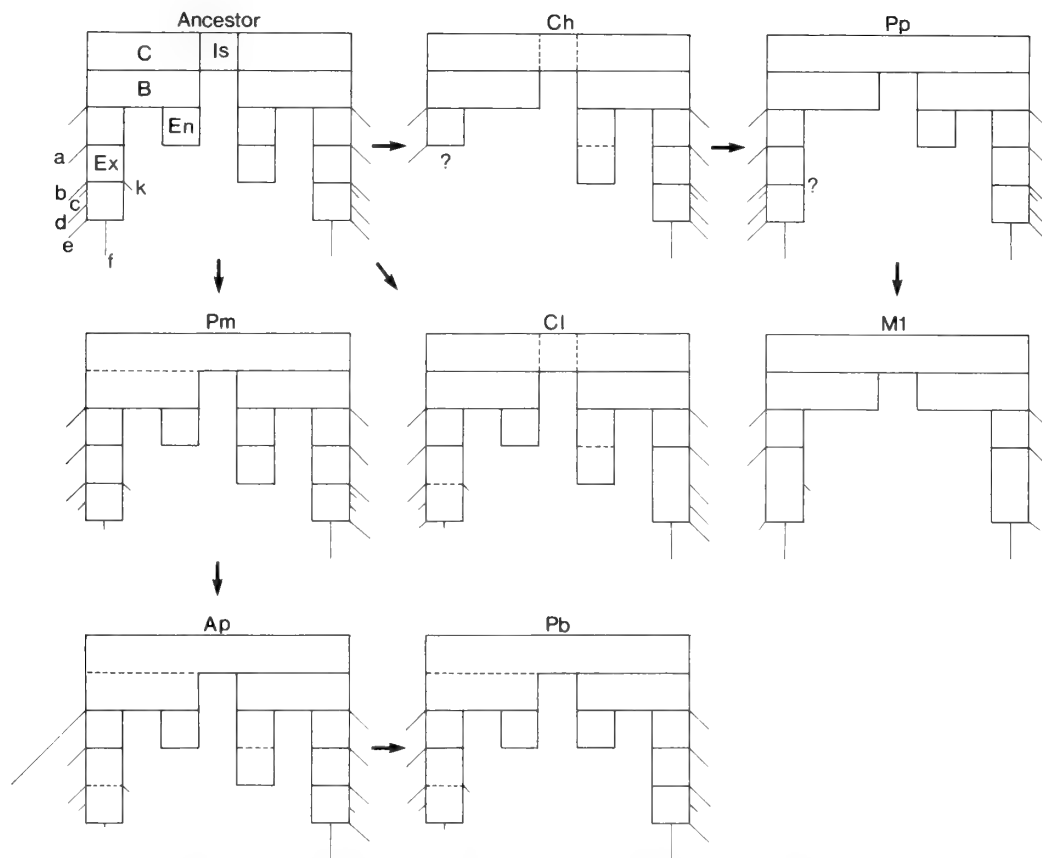


Fig. 43. Schematic comparison of segmentation and setation of male fifth legs in the Arietellidae. The arrows indicate possible derivations of setation and segmentation patterns and are not indicative of ancestor-descendant relationships between taxa. Ch: *Crassarietellus huysii*; Pp: *Paramisophria platysoma*; Pm: *Paraugaptiloides magnus*; Cl: *Campaneria latipes*; M1: *Metacalanus* species 1; Ap: *Arietellus plumifer*; Pb: *Paraugaptilus buchani*. C: Coxa; B: Basis; Is: Intercoxal sclerite; Ex: Exopod; En: Endopod. a-f, k: elements on exopod. Setae and spines are not distinguished here.

The intercoxal sclerite and both coxae are almost fused, with the suture clearly visible in *Crassarietellus* and *Campaneria*, while in the other genera fusion is complete. The basis and coxa are completely separate in both legs in *Crassarietellus*, *Campaneria*, *Paramisophria* and *Metacalanus*, almost completely fused in the right leg but completely separate in the left leg in *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*.

Phylogenetic relationships between arietellid genera

Phylogenetic relationships between the 10 genera studied in this paper were analyzed using PAUP 3.0 on a matrix of 44 characters (Tables 2,3). The matrix contains a significant proportion of missing data, shown in the matrix by a '9' (Table 3). These missing data correspond to the unknown males of the genera *Scutogerus*, *Sarsarietellus* and *Pilarella* and to the unknown females of *Campaneria* and *Paraugaptiloides*. Since most of the characters used in the analysis are sexually dimorphic (30 out of 44 characters), only a minority of characters (14 of 44) can be scored for all taxa. The phylogenetic scheme presented here is necessarily tentative, subject to re-examination as the gaps in the data matrix are filled by the discovery of unknown sexes.

Four trees were generated by the analysis, all with the same

statistics: tree length = 179; consistency index = 0.263; homoplasy index = 0.737. These four trees differed only in the relative positions of *Campaneria*, *Paraugaptiloides* and *Sarsarietellus*. The relative positions of all other genera are the same. All three of these genera are known from only one sex. Tree 1 (Fig. 44) was selected as the best working hypothesis of relationships because *Campaneria* was the first offshoot of the *Arietellus*-group, as it was in three of the four trees, and because it placed *Sarsarietellus* as an earlier offshoot than *Paraugaptiloides* which we consider to be the more apomorphic genus of the two.

The genera of the Arietellidae form two lineages, the *Arietellus*-group comprising six genera, and the *Metacalanus*-group consisting of four genera. The *Arietellus*-group is diagnosed by the apomorphic reduction of seta a on the terminal segment of the maxillipedal endopod (character 27). The *Metacalanus*-group lacks a simple diagnostic character. The apomorphic state of character 38 (absence of endopod of male right fifth leg) is found only within the group, in *Crassarietellus*, *Paramisophria* and *Metacalanus* (the male of *Pilarella* is unknown), and the apomorphic state of character 3 (asymmetrical antennules in females) is found only in *Paramisophria*, *Metacalanus* and *Pilarella*. *Crassarietellus* retains the plesiomorphic state.

This analysis suggests that there may have been several

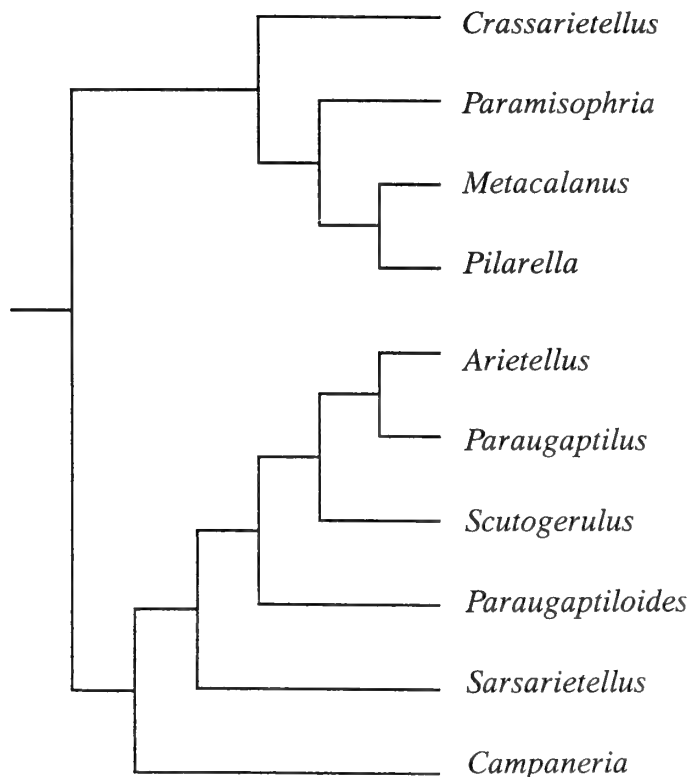


Fig. 44. Cladogram depicting relationships among arietellid genera.

shifts in habitat utilization during the evolutionary history of the family. Substitution of habitat type (Fig. 45) onto the cladogram shown in Fig. 44 indicates that the Arietellidae originated in the hyperbenthic zone. The most plesiomorphic representatives of both lineages still inhabit this zone. The *Metacalanus*-group has largely remained in the ancestral hyperbenthic habitat although it has successfully colonized anchialine caves (Ohtsuka et al., 1993a) and at least one species of *Metacalanus* is epipelagic. In contrast, the most apomorphic representatives of the *Arietellus*-group, the genera *Arietellus* and *Paraugaptilus*, have successfully colonized the open pelagic realm.

A similar analysis of habitat utilization was performed on the genera of the copepod family Misophriidae by Boxshall (1989). The 10 genera of this family were placed in two lineages, both of which originated in the deep-water hyperbenthic zone. The first offshoot of the *Archimisophria*-lineage, represented by the genus *Archimisophria* Boxshall, 1983, has remained in the ancestral habitat but all the derived representatives of this lineage are found in anchialine caves and crevicular habitats. The most plesiomorphic representative of the *Misophria*-lineage, the genus *Misophriopsis* Boxshall, 1983, also inhabits the hyperbenthic zone but other members of the lineage have successfully colonized the pelagic zone, the shallow-water hyperbenthic zone and, independently, anchialine habitats.

There are interesting parallels between the Arietellidae and Misophriidae. The ancestry of both families appears to be closely associated with the deep-water hyperbenthic zone. Plesiomorphic genera in both families have remained in the ancestral habitat but more derived representatives now utilize a broader spectrum of habitat types, including the shallow-

water hyperbenthic zone, the open pelagic realm and anchialine caves. Certain habitat shifts appear to have occurred at least twice, independently, within these two families. The colonization of anchialine habitats appears to have taken place twice in the Arietellidae, once within *Metacalanus* and once within *Paramisophria*, just as Boxshall (1989) found for the Misophriidae. Arietellids appear to have invaded the open pelagic zone three times (the *Arietellus*-*Paraugaptilus* group, *Paraugaptiloides*, and within the genus *Metacalanus*).

Key to genera of the family Arietellidae

- 1a Leg 1 with 1 outer spine on third exopod segment 2
- 1b Leg 1 with 2 outer spines on third exopod segment 3
- 2a Maxillule with 5 spines and 1 process on praecoxal arthrite; maxilla with 1 seta on distal praecoxal endite; caudal seta II developed; genital double-somite (♀) with paired genital system, each copulatory pore opening within slit-like genital slit, shared with gonopore *Scutogerulus* Bradford, 1969
- 2b Maxillule with 5 spines and 1 process on praecoxal arthrite; maxilla with 2 setae on distal praecoxal endite; caudal seta II developed; genital double-somite (♀) with paired genital system, each copulatory pore opening within common genital aperture, shared with gonopore *Pilarella* Alvarez, 1985
- 2c Maxillule with 0–2 elements on praecoxal arthrite; maxilla with 2 setae on distal praecoxal endite; caudal seta II reduced; genital double-somite (♀) with gonopore and copulatory pore separate and located posteriorly *Metacalanus* Cleve, 1901
- 3a Maxillule with 6 setae on coxal epipodite 4
- 3b Maxillule with 8–9 setae on coxal epipodite 5

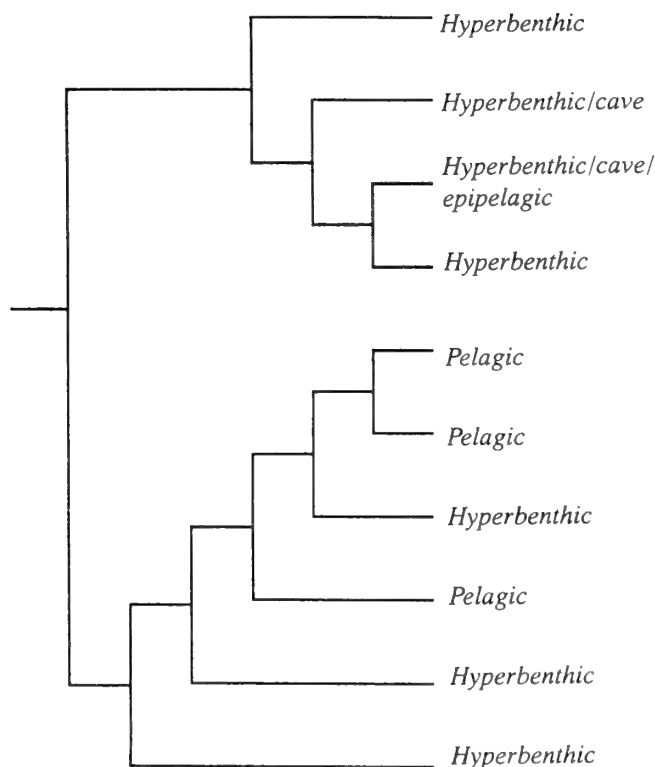


Fig. 45. Habitat cladogram of arietellid genera. Substitution of habitat type of each genus onto cladogram shown in Fig. 44.

4a Antennary exopod indistinctly 10-segmented; maxillary praecoxal arthrite with strongly serrate spines; long innermost seta on fifth endopod segment of maxilliped; outermost seta on sixth endopod segment of maxilliped not reduced; left antennule (♂) with 2 setae on segments II and III, and segments XXI and XXII fused; right endopod of leg 5 (♂) lacking
..... *Crassarietellus* gen. nov.

4b Antennary exopod indistinctly 8-segmented; maxillary praecoxal arthrite with weakly serrate spines; short innermost seta on fifth endopod segment of maxilliped; outermost seta on sixth endopod segment of maxilliped reduced; left antennule with 1 seta on segments II and III, and segments XXI and XXII separate; right endopod of leg 5 (♂) present
..... *Campaneria* gen. nov.

5a Innermost seta on fourth and fifth endopod segments of maxilliped vestigial *Arietellus* Giesbrecht, 1892

5b Innermost seta on fourth and fifth endopod of maxilliped not vestigial 6

6a Antennary exopod segment X unarmed
..... *Paraugaptilus* Wolfenden, 1904

6b Antennary exopod segment X with 3 elements 7

7a Leg 4 with inner coxal seta; second antennary endopod segment with 2 inner setae at midlength *Paraugaptiloides* gen. nov.

7b Leg 4 without inner coxal seta; second antennary endopod segment with 3 inner setae at midlength 8

8a Antennular segments XXV and XXVI separated; basal spine of maxilla ornamented with spinules; outermost seta on sixth endopod segment of maxilliped vestigial; genital double-somite (♀) with copulatory pore located midventrally on median line or on left side; copulatory duct heavily chitinized; seminal receptacle elongate, its distal end bulbous in shape; inner process

(derived from endopod) of leg 5 (♀) with 4 setae

..... *Sarsarietellus* Campaner, 1984

8b Antennular segments XXV and XXVI fused; basal spine of maxilla bare; outermost seta on sixth endopod segment of maxilliped not vestigial; genital double-somite (♀) with copulatory pore located posteroventrally; seminal receptacle not elongate, its distal end not bulbous; inner process of leg 5 (♀) with 0–2 setae *Paramisophria* T. Scott, 1897

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Whenever possible a copy of the text, once the paper has been accepted, should also be provided on floppy disc (see below). Discs should only be sent after final acceptance, as papers generally need revision after refereeing. If it is impossible to provide an appropriate disc please ensure that the final typescript is clearly printed.

Authors are requested to ensure that their manuscripts are in final format, because corrections at proof stage may be charged to the author. Additions at proof stage will not normally be allowed. Page proofs only will be sent.

Word-processor discs. Please follow these instructions.

1. Ensure that the disc you send contains only the final version of the paper and is identical to the typescript.

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4. Specify any unusual non-keyboard characters on the front page of the hard copy.

5. Do not right-justify the text.

6. Do not set a left-hand margin.

7. Make sure you distinguish numerals from letters, e.g. zero (0) from O; one (1) from l (el) and I.

8. Distinguish hyphen, en rule (longer than a hyphen, used without a space at each end to signify 'and' or 'to', e.g. the Harrison-Nelson technique, 91-95%, and increasingly used with a space at each end parenthetically), and em rule (longer than an en rule, used with a space at each end parenthetically) by: hyphen, two hyphens and three hyphens, respectively. Be consistent with rule used parenthetically.

9. Use two carriage returns to indicate beginnings of paragraphs.

10. Be consistent with the presentation of each grade of heading (see **Text** below).

Title. The title page should be arranged with the full title; name(s) of author(s) without academic titles; institutional address(es); suggested running title; address for correspondence.

Synopsis. Each paper should have an abstract not exceeding 200 words. This should summarise the main results and conclu-

sions of the study, together with such other information to make it suitable for publication in abstracting journals without change. References must not be included in the abstract.

Text. All papers should have an Introduction, Acknowledgements (where applicable) and References; Materials and Methods should be included unless inappropriate. Other major headings are left to the author's discretion and the requirements of the paper, subject to the Editors' approval. Three levels of text headings and sub-headings should be followed. All should be ranged left and be in upper and lower case. Supra-generic systematic headings only should be in capitals; generic and specific names are to be in italics, underlined. Authorities for species names should be cited only in the first instance. Footnotes should be avoided if at all possible.

References. References should be listed alphabetically. Authorities for species names should not be included under References, unless clarification is relevant. The author's name, in bold and lower case except for the initial letter, should immediately be followed by the date after a single space. Where an author is listed more than once, the second and subsequent entries should be denoted by a long dash. These entries should be in date order. Joint authorship papers follow the entries for the first author and an '&' should be used instead of 'and' to connect joint authors. Journal titles should be entered in full. Examples: (i) Journals: England, K.W. 1987. Certain Actinaria (Cnidaria, Anthozoa) from the Red Sea and tropical Indo-Pacific Ocean. *Bulletin of the British Museum (Natural History)*, Zoology 53: 206-292. (ii) Books: Jeon, K.W. 1973. *The Biology of Amoeba*. 628 p. Academic Press, New York & London. (iii) Articles from books: Hartman, W.D. 1981. Form and distribution of silica in sponges. pp. 453-493. In: Simpson, T.L. & Volcani, B.E. (eds) *Silicon and Siliceous Structures in Biological Systems*. Springer-Verlag, New York.

Tables. Each table should be typed on a separate sheet designed to extend across a single or double column width of a Journal page. It should have a brief specific title, be self-explanatory and be supplementary to the text. Limited space in the Journal means that only modest listing of primary data may be accepted. Lengthy material, such as non-essential locality lists, tables of measurements or details of mathematical derivations should be deposited in the Biological Data Collection of the Department of Library Services, The Natural History Museum, and reference should be made to them in the text.

Illustrations. Figures should be designed to go across single (84 mm wide) or double (174 mm wide) column width of the Journal page, type area 235 × 174 mm. Drawings should be in black on white stiff card or tracing film with a line weight and lettering suitable for the same reduction throughout, either 50%, 30% or 25%. After reduction the smallest lettering should be not less than 10 pt (3 mm). All photographs should be prepared to the final size of reproduction, mounted upon stiff card and labelled with press-on lettering. Components of figure-plates should be abutted. All figures should be numbered consecutively as a single series. Legends, brief and precise, must indicate scale and explain symbols and letters.

Reprints. 25 reprints will be provided free of charge per paper. Orders for additional reprints can be submitted to the publisher on the form provided with the proofs. Later orders cannot be accepted.

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